Evolution of the Orthoptera: systematic placement among insects, internal phylogeny and the origin of bioacoustics

Dissertation

zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades

“Doctor rerum naturalium“

der Georg-August-Universität Göttingen

im Promotionsprogramm Biologie

der Georg-August University School of Science (GAUSS)

vorgelegt von

Fanny Leubner

aus Dresden

Göttingen, 2017

Betreuungsausschuss:

PD Dr. Sven Bradler, Abteilung Morphologie, Systematik & Evolutionsbiologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

Prof. Dr. Rainer Willmann, Abteilung Morphologie, Systematik & Evolutionsbiologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

Mitglieder der Prüfungskommission:

Referent: PD Dr. Sven Bradler, Abteilung Morphologie, Systematik & Evolutionsbiologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

Korreferent: Prof. Dr. Rainer Willmann, Abteilung Morphologie, Systematik & Evolutionsbiologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

Weitere Mitglieder der Prüfungskommission:

Prof. Dr. Andreas Stumpner, Abteilung Zelluläre Neurobiologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

Prof. Dr. Ralf Heinrich, Abteilung Zelluläre Neurobiologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

PD Dr. Nikola-Michael Prpic-Schäper, Abteilung Entwicklungsbiologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

Prof. Dr. Mark Maraun, Abteilung Tierökologie, J.-F.-Blumenbach Institut für Zoologie und Anthropologie, Georg-August-Universität Göttingen

Tag der mündlichen Prüfung: 7.7. 2017

AFFIDAVIT

I hereby declare that the doctoral thesis entitled,

„Evolution of the Orthoptera: systematic placement among insects, internal phylogeny and the origin of bioacoustics“

has been written independently and with no other sources and aids than quoted.

I have not submitted this thesis in any form for another degree at any university or institution.

Fanny Leubner Göttingen, May 9th , 2017

So eine Arbeit wird eigentlich nie fertig, man muß sie für fertig erklären, wenn man nach Zeit und Umständen das Möglichste getan hat.

Johann Wolfgang von Goethe

Contents

CHAPTER 2

Summary

The present thesis provides (1) a detailed study of the yet neglected skeletomuscular complex of the thorax in Orthoptera, (2) a comparative study of the morphological modifications associated with secondary winglessness in polyneopteran lineages and Ensifera in particular, (3) a phylogenetic reconstruction of ensiferan relationships based on characters of the thoracic skeleton and musculature, and in light of the aforementioned results (4) a reinterpretation of the evolutionary origin of bioacoustics within Ensifera.

The thoracic skeletomuscular complex of 23 orthopteran species was studied in detail, including representatives of all major ensiferan lineages. This comprehensive comparative approach served as a basis for a thorough reconstruction of the potential ground pattern of the orthopteran thoracic skeleton and musculature. Both skeletal and muscular morphology of the thorax show major differences between the two basal orthopteran sublineages Caelifera (short-horned grasshoppers) and Ensifera (long-horned grasshoppers). Secondary winglessness, a widespread phenomenon among pterygote insects, largely affects the thoracic anatomy, mainly the skeletal structures and the muscular system. By comparing the thoracic morphology of various wingless representatives of Polyneoptera, it can be demonstrated that anatomical adaptations towards flightlessness, especially regarding the flight musculature, are highly homogenous within major insect lineages, viz. Ensifera, Caelifera, and the majority of stick and leaf insects (Euphasmatodea). However, specific adaptations differ strikingly between these major lineages indicating different roles and functions of these muscles after wing loss.

The cladistic analysis of 141 thoracic characters for the examined orthopterans and outgroup representatives of all major polyneopteran lineages, Holometabola, Paraneoptera and Palaeoptera yielded a single most parsimonious phylogenetic tree. Within Polyneoptera that were recovered as monophyletic a close relationship of Orthoptera to a clade comprising Xenonomia (Grylloblattodea + Mantophasmatodea), Dictyoptera, and Phasmatodea is supported. Ensifera is divided into two major lineages: a grylloid clade (crickets and mole crickets) and a tettigonioid clade (bush-crickets and relatives). Tettigoniidae is found to be the sister taxon of a clade comprising Gryllacrididae, Schizodactylidae, Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae. The monophyly of the latter

clade is supported by a pronounced posterior profurcal arm (convergent in Grylloblattodea) and a paired posterior processus of the stalked prospina (with a reversal assumed for Prophalangopsidae). Additional key findings on internal ensiferan relationships and their resulting interpretation for the evolution of bioacoustics are briefly outlined in the following: (1) Prophalangopsidae is not forming the sister group to Tettigoniidae. The presence of a tegminal stridulatory apparatus as an intraspecific communicational form must have evolved independently in at least three lineages: Gryllidae + Gryllotalpidae, Tettigoniidae, and Prophalangopsidae. (2) Rhaphidophoridae is not forming the sister group to the remaining tettigonioid lineages, instead a close relationship to Prophalangopsidae, Anostostomatidae and Stenopelmatidae is proposed based on the presence of a unique triramous metafurca in these taxa. The previous hypothesis of a basal position of Rhaphidophoridae within the tettigonioid clade supported a scenario of a non-stridulating and non-hearing ensiferan ancestor, and indicated a step-wise evolution of the hearing organs and intraspecific stridulatory mechanisms towards singing and hearing ensiferans such as katydids. Based on the novel hypothesis, the structure of the rhaphidophorid hearing organ bearing no crista acustica must instead be a consequence of secondary simplification. (3) Tettigoniidae, Prophalangopsidae and Anostostomatidae do not form a monophylum. The occurrence of acoustic intraspecific communication, either in form of tegminal or femoro-abdominal stridulation, does therefore not represent a plesiomorphic condition for each of these three taxa, but rather constitutes an independently evolved new (apomorphic) condition for or within each lineage.

In summary, the present thesis increases the knowledge on the morphology of a complex anatomical character system. This thesis represents an essential step towards a deeper understanding of the evolution of thoracic characters and related functional adaptations within insects, and Polyneoptera and Orthoptera in particular. Despite the fact that studies analyzing morphological data are nowadays mainly replaced by those providing robust molecular phylogenetic hypotheses, morphological research remains an important instrument to make evolution more comprehensible and explains form and function of morphological transformations in evolutionary history.

General Introduction

Since the last decades, researchers devoted their expertise to gain a deeper knowledge on the morphology, neurobiology, behaviour and ecology of grasshoppers, crickets, katydids and their allies. With more than 27 500 described extant species, Orthoptera (or Saltatoria) forms one of the most species-rich lineage among the lower neopteran insects (Grimaldi & Engel 2005; Eades *et al.* 2015). Besides the polar regions, orthopterans inhabit all continents and show an overwhelming abundance in diversity and in the range of occupied terrestrial habitats (Beier 1972; Kevan 1982). The monophyly of Orthoptera

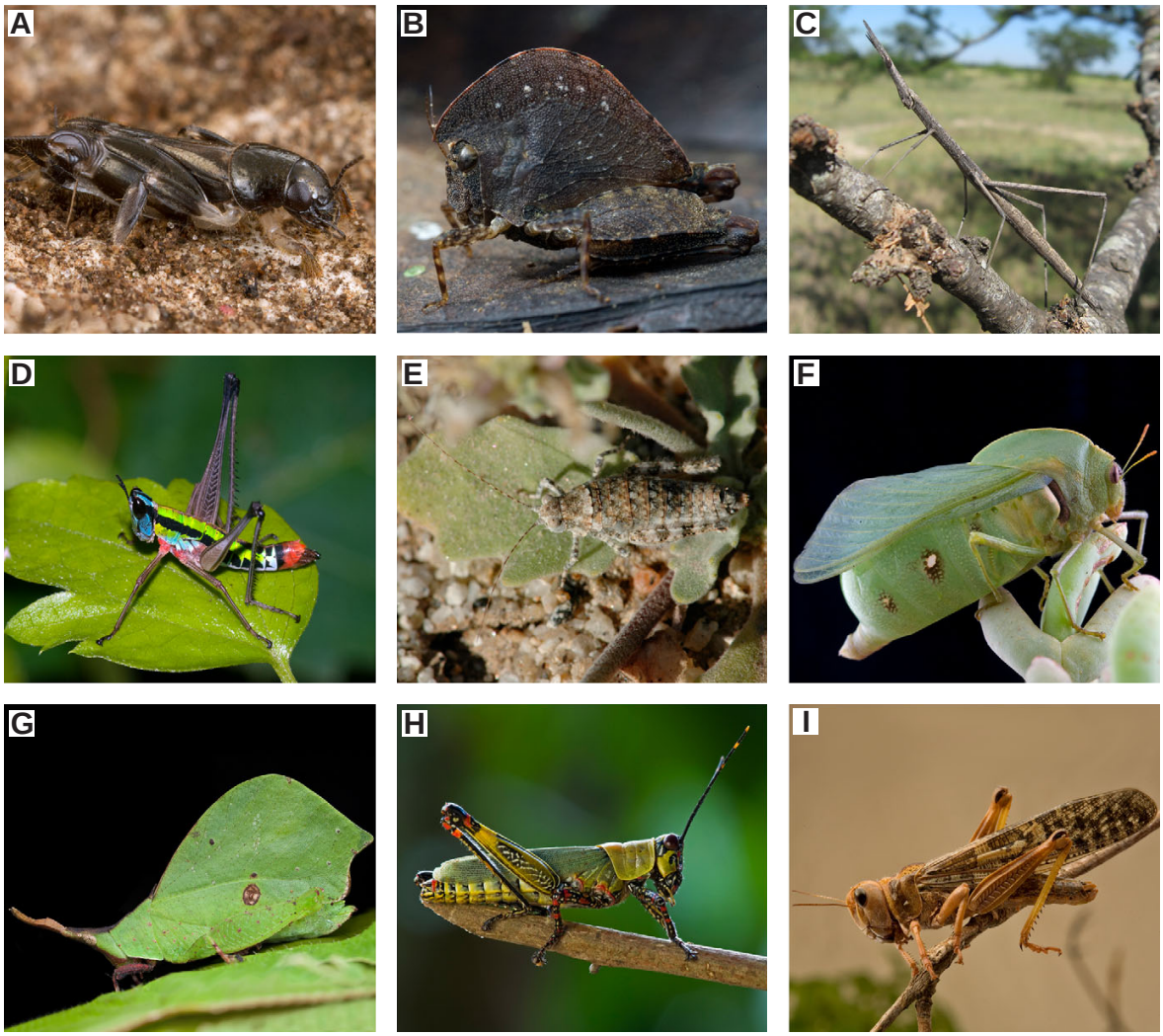


Figure 1. Representatives of Caelifera. (A) Tridactylidae: *Xya* sp., (B) Tetrigidae: *Afrolarcus* sp., (C) Proscopiidae: *Tetanorhynchus* sp., (D) Episactidae: *Episactus tristani*, (E) Tanaoceridae: *Tanaocerus koebelei*, (F) Pneumoridae: *Bullacris* sp., (G) Trigonopterygidae: *Systella rafflesii*, (H) Pyrgomorphidae: *Zonocerus variegatus*, (I) Acrididae: *Locustana pardalina*; from Song *et al.* 2015. (Photo credit: Piotr Naskrecki [A, B, F, H, I], Paul Lenhart [C], Robert A. Behrstock [D], Hartmut Wisch [E], Kurt Orion [G]).

is rarely doubted (Sharov 1968) and appears well supported by some morphological characters, such as the large saddle-shaped pronotum, an internal cryptopleura, and the saltatorial hind legs that exhibit a straightened femur-tibia articulation in combination with a conceivable reduction of the trochanter (Kristensen 1991; Grimaldi & Engel 2005; Kluge 2016). Orthoptera is subdivided into two major lineages: Caelifera (short-horned grasshoppers: locusts, grasshoppers and allies) (Fig. 1) and Ensifera (long-horned grasshoppers: crickets, katydids, wetas and allies) (Fig. 2).

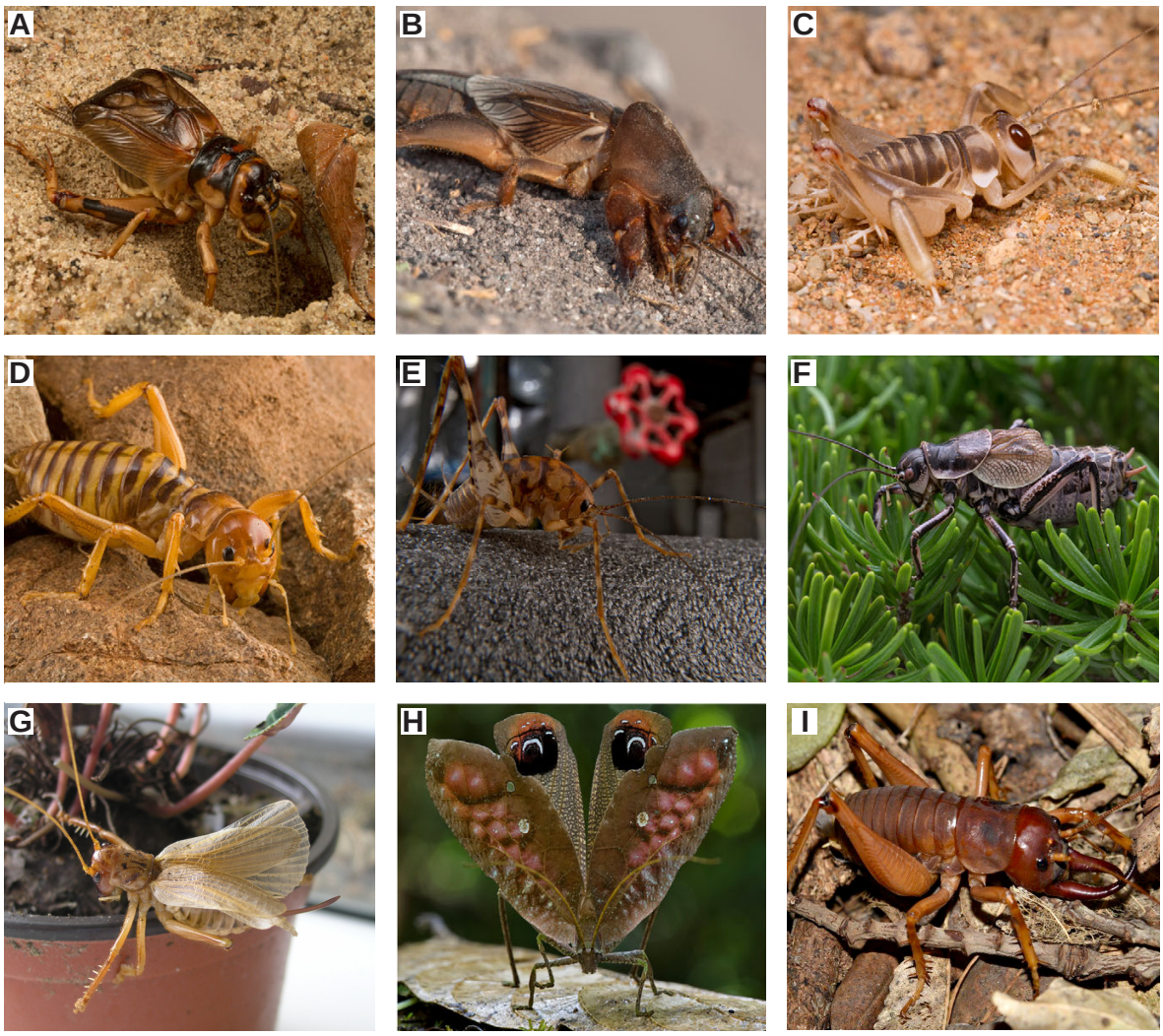


Figure 2. Representatives of Ensifera. (A) Gryllidae: *Brachytrupes membranaceus*, (B) Gryllotalpidae: *Gryllotalpa africana*, (C) Schizodactylidae: *Comicus capensis*, (D) Stenopelmatidae: *Sia* sp., (E) Rhaphidophoridae: *Diestrammena asynamora*, (F) Prophalangopsidae: *Cyphoderris monstrosa*, (G) Gryllacrididae: *Pterapotrechus* sp., (H) Tettigoniidae: *Pterochroza ocellata*, (I) Anostostomatidae: *Motuweta isolata*; modified from Song *et al.* 2015. (Photo credit: Piotr Naskrecki [A, B, C, D, E, F, H], Auckland War Memorial Museum [G, subsequently added], Rob Chappell [I, subsequently added].

Systematic placement of Orthoptera among Neoptera

The Neoptera, insects that are capable of folding their wings over the abdomen, are traditionally subdivided in three main groups: Holometabola (characterized by a pupal stage and a complete metamorphosis), Paraneoptera (characterized by sucking mouth parts), and a third group termed 'Lower Neoptera' or 'Polyneoptera'. Whereas there is no doubt about the monophyly of Holometabola (e.g. Beutel *et al.* 2011; Misof *et al.* 2014), the assumption of monophyletic Paraneoptera and Polyneoptera was controversially discussed in the past (reviewed in Trautwein *et al.* 2012; Yeates *et al.* 2012). Numerous phylogenetic studies before 2011 arrived at topologies of the lower neopteran lineages that widely agreed on paraphyletic Polyneoptera (Kjer 2004; Yoshizawa & Johnson 2005; Terry & Whiting 2005; Beutel & Gorb 2006). Due to the improved access to huge amounts of molecular data and novel methods to analyze this genetic information the number of insect phylogenetic studies has strongly increased after 2011. Interestingly, these more recent phylogenetic studies that are based on quite different data types, e.g. mitochondrial DNA, ribosomal DNA, whole genomes, transcriptomes, and also morphology, support monophyletic Polyneoptera (e.g. Ishiwata *et al.* 2011; Letsch & Simon 2013; Misof *et al.* 2014; Wipfler *et al.* 2015; Song *et al.* 2016). Unfortunately, the internal relationships among the major polyneopteran lineages in particular remained poorly understood, which likely is a consequence of their ancient rapid radiation (Whitfield & Kjer 2008). These basal splitting events are difficult to resolve because of the short branches between lineages that hardly allows the formation of synapomorphic characters. The Polyneoptera comprises 11 major lineages: praying mantises (Mantodea), cockroaches (Blattodea), termites (Isoptera), earwigs (Dermaptera), stick and leaf insects (Phasmatodea), webspinners (Embioptera), stoneflies (Plecoptera), angel insects (Zoraptera), ice crawlers (Grylloblattodea), grasshoppers and relatives (Orthoptera), and heel walkers (Mantophasmatodea), a polyneopteran taxon only discovered as recent as 2002 (Klass *et al.* 2002). Among Polyneoptera, several monophyletic entities were repeatedly proposed based on the analysis of different types of data. These include the taxa Dictyoptera (comprising Mantodea, Blattodea and Isoptera), Xenonomia (Mantophasmatodea + Grylloblattodea), and Eukinolabia (Phasmatodea + Embioptera). The current knowledge on

the relationships among the three main groups of Neoptera, and its internal relationships is summarized in Fig. 3.

Besides a few phylogenetic studies based on 18S and 28S rDNA, in which Orthoptera were found to be the sister group to Holometabola (Yoshizawa & Johnson 2005; Wang *et al.* 2013), the phylogenetic affinity of Orthoptera to Polyneoptera was repeatedly confirmed in morphology and molecular data based phylogenies. Nevertheless, the phylogenetic placement of Orthoptera among Polyneoptera appears unstable across analyses and widely varies in proposed phylogenies, which either assume orthopterans to be close relatives of a single major polyneopteran lineage, like e.g. Phasmatodea (Beutel & Gorb 2006; Yoshizawa 2011), or rather an affinity to a whole group of quite a few polyneopteran

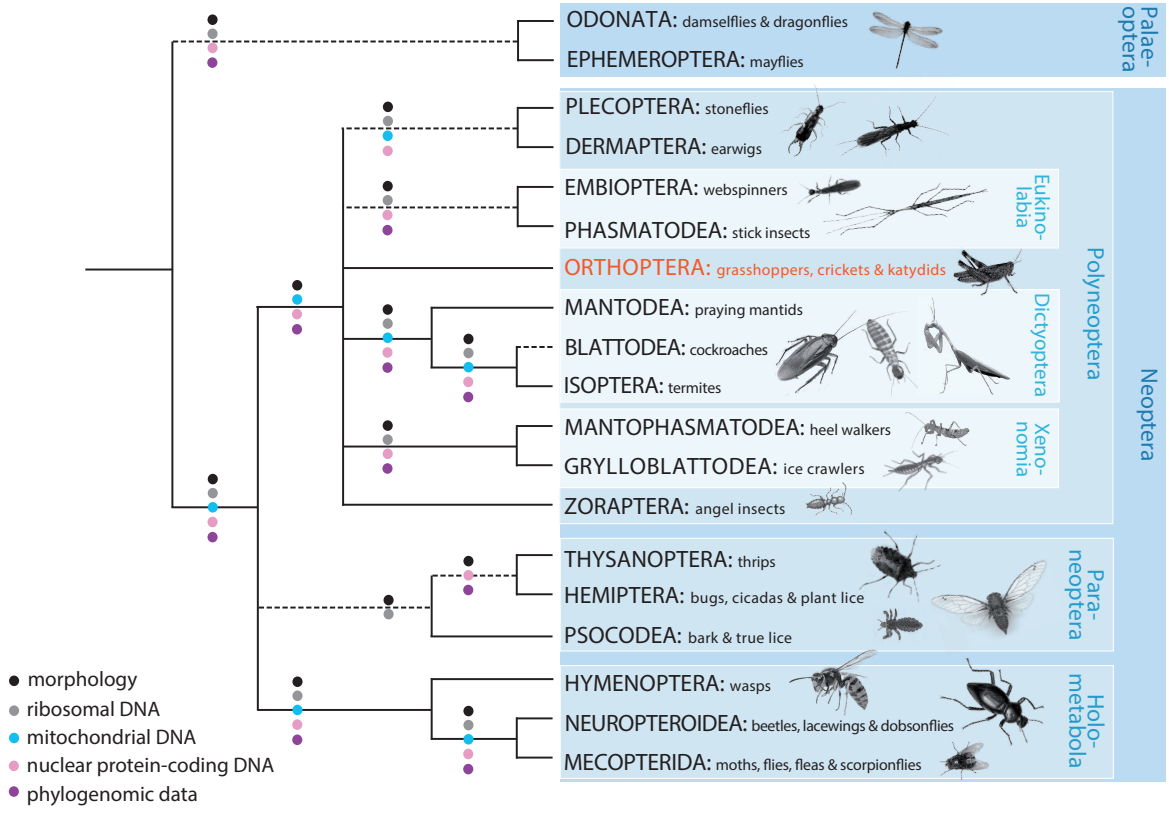


Figure 3. Current view of the of pterygotan relationships based on a review of recent studies. Strongly modified from Trautwein *et al.* 2012, including results of phylogenetic studies after 2012. Dashed lines indicate tenuously supported relationships or possible nonmonophyly (in terminal branches). Data types that support a node are given when a node was recovered by data type alone or in combined analyses.

lineages (Misof *et al.* 2014; Song *et al.* 2016). These circumstances currently hamper the choice of an ideal single outgroup taxon for cladistic analyses of Orthoptera and call for the inclusion of representatives of preferably all major polyneopteran lineages.

Internal relationships of long-horned grasshoppers (Ensifera)

Traditional classifications of Ensifera are based on a single character system, the morphology of the wings and wing venation in particular (Zeuner 1939; Ragge 1955; Sharov 1968). Ander (1939) was the first author discussing different morphological character systems, e.g. head, thorax, prothoracic musculature, tracheal and digestive system, in a comprehensive approach for a vast number of ensiferan taxa. Ander's work was truly ahead of its time, as his conclusions on the internal relationships of Ensifera were exclusively based on shared derived characters and, in addition, his work was published roughly ten years before Hennig (1950) formulated his fundamentals of phylogenetic systematics. Ander assumed the Ensifera to be divided into two major lineages: mainly crickets (Gryllidae) and mole crickets (Gryllotalpidae) on one side, and on the other side a lineage comprising cave crickets (Rhaphidophoridae), dune crickets (Schizodactylidae), raspy crickets (Gryllacrididae), Jerusalem crickets, king crickets and wetas (his 'Stenopelmatidae' include the members of the Anostostomatidae), hump-winged crickets (Prophalangopsidae), and katydids (Tettigoniidae). This major split of Ensifera into a 'grylloid clade' and a 'tettigonioid clade' gained further evidence in subsequent formal cladistic analyses (Desutter-Grandcolas 2003; Song *et al.* 2015; Zhou *et al.* 2017). Nevertheless, the internal relationships of the 'tettigonioid' clade and in particular the systematic placement of dune crickets were proposed in at least partly drastically different phylogenetic hypotheses. Although ensiferan taxonomy was based on a wealth of morphological characters, until now only two formal cladistic analyses based on morphological data have been conducted to infer the internal relationships. Gwynne (1995) mainly adopted data from taxonomic literature and coded 67 morphological characters to address questions on the evolution of mating behaviour and acoustic communication within the Ensifera. However, Gwynne's approach was sharply criticized for its flawed methodology (Nickle & Naskrecki 1997; Desutter-Grandcolas 2003), suffering from errors and imprecision in character coding, especially for hypotheses of primary homology (Desutter-Grandcolas 2003). The approach

of Desutter-Grandcolas (2003) was based on 85 morphological characters including different character systems such as the thorax, tegmina and wings, legs, genitalia, and the nervous system. Desutter-Grandcolas coded these characters for 12 supraspecific terminal taxa, whereby data of groups on the 'family' level (e.g. Tettigoniidae, Stenopelmatidae) were compared with that on the generic level (e.g. *Cyphoderris*, *Prophalangopsis*, *Lezina*). Both aforementioned studies are closely linked to the question of the origin and evolution of bioacoustics within the Ensifera. Orthoptera in general have long been of interest to scientists studying acoustic communication and hearing systems (Robinson & Hall 2002). Acoustic communication between conspecifics is widespread in this insect lineage, and also specialized hearing organs occur frequently in both subgroups (Beier 1972). When developed, the hearing organs of caeliferans are typically localized in the first abdominal segment (Yack 2004), whereas that of ensiferans is situated in the tibia of the forelegs (Yack 2004) with its tympanum in most cases visible from the outside (Fig. 4).

Especially the acoustic signalling and sound processing of crickets (Gryllidae) and bush-crickets or katydids (Tettigoniidae) that communicate by a rapid friction of the forewings (tegminal stridulation) are popular model systems with widespread interest among researchers (e.g. Gwynne 2001; Korsunovskaya 2008; Strauß *et al.* 2014). As the consequence of a communicating system quite similar to that of katyids, hump-winged crickets (Prophalangopsidae) were traditionally placed as the sister taxon to Tettigoniidae, since members of both families are capable of tegminal stridulation and perceiving sounds by means of a functional tympanal organ on the fore tibiae. By including characters of acoustic communication into their character matrices, both Gwynne (1995) and Desutter-Grandcolas (2003) proposed a monophyletic origin of hump-winged crickets and katydids. In contrast to the alternate opinion of a single evolutionary origin of tegminal stridulation in the last common ancestor of all Ensifera (Alexander 1962; Otte 1992), these phylo-

Figure 4. Southern oak bush-cricket (*Meconema meridionale*). The tympanum of the tibial organ is visible from the exterior at its left foreleg. (Photo credit: Fanny Leubner).

genetic schemes obtained from morphological data likely support an independent origin of tegminal stridulation in at least two lineages: in crickets + mole crickets, and in hump-winged crickets + katydids (Gwynne 1995; Desutter-Grandcolas 2003). However, all large-scale phylogenetic studies based on molecular data reject a sister group relationship of Prophalangopsidae and Tettigoniidae, and instead place Prophalangopsidae in close relation to Jerusalem crickets (Stenopelmatidae), king crickets (Anostostomatidae) and/or raspy crickets (Gryllacrididae) (Jost & Shaw 2006; Legendre *et al.* 2010; Song *et al.* 2015; Zhou *et al.* 2017). Unfortunately, none of these studies drew concrete conclusions on the resulting consequences for the evolution of bioacoustics within Ensifera, and a critical reanalysis of this character system is of crucial importance to review and evaluate the compatibility of hypotheses of the evolutionary origin of ensiferan bioacoustics with the currently hypothesized phylogenetic relationships.

Thoracic morphology of Orthoptera

In general, the insect thorax is composed of three segments: pro-, meso- and metathorax (Snodgrass 1935). The insect thorax represents the 'centre of locomotion', since each segment bears a pair of legs and in the Pterygora the posterior two most likely bear wings (Snodgrass 1935). All of these segments are characterized by external skeletal elements, sclerites, that either stabilize the dorsal (terga or tergites), lateral (pleura or pleurites) or ventral (sterna or sternites) part of the thorax (Snodgrass 1935). As much as bones in the human body, the chitinous sclerites of the insect's external skeleton serve as attachment points for musculature and thereby enable a variety of complex movements, like running, jumping or even flying. Indeed, the evolution of wings in Pterygota is considered to be a key factor that is responsible for the unrivalled evolutionary success of insects, improving dispersal capability, predator avoidance, as well as the access to scattered food sources and mating partners (Wagner & Liebherr 1992). Beyond flight, wings are shown to provide several additional advantages, such as a contribution to thermoregulation, defensive behaviour and acoustic communication (Edmunds 1974; Kingsolver 1985; Robinson & Hall 2002). Nevertheless, wing loss is a common phenomenon among pterygote insects (Wagner & Liebherr 1992) and may be accompanied by several radical modifications of the insect thorax: the reduction of wing base sclerites, less extensive phragmata, and

the partial or complete reduction of flight-associated muscles (Maki 1938; Ewer 1954). Orthoptera represents an insect lineage in which up to 50% of the known species are flightless (Roff 1994). Within the Ensifera, wings are either absent in whole lineages, as in cave crickets (Rhaphidophoridae) or ant-loving crickets (Myrmecophilidae) (Beier 1972), or only in isolated genera or species within a certain group, as in the dune cricket genus *Comicus* (Schizodactylidae) (Irish 1986). It is apparent that wings must have been lost several times independently in the evolutionary history of Neoptera and in Orthoptera in particular. Wing reduction and loss is a stepwise process with numerous morphological transformations in each lineage. There are still many outstanding questions related to general adaptations of the thoracic skeletal and muscular system in wingless insects and their thoracic functional anatomy. Do the transformations in each wingless insect follow the same pattern? Or is independent wing loss anatomically traceable with specific differences retained in the morphology of the thorax?

Already back in 1939, Kjell Ander stated that skeletal and muscular features of the ensiferan thorax are highly informative for understanding phylogenetic relationships of this diverse taxon. Next to characters such as the prothoracic cryptopleura, the form of the first thoracic spiracle, certain muscle characters of the prothorax as well as the external shape and structure of the sternites, Ander assigned the internal sternal skeleton to "offer excellent anatomical characters" ("*Das sternale innere Skelett bietet ebenfalls vortreffliche Merkmale.*" Ander 1939). Nonetheless, besides little fragmentary information on the specific structure of the furcae, internal apophyses of the sternites, of crickets and Jerusalem crickets, Ander abstained from a detailed and comprehensive description in other ensiferan taxa. Until today, the thoracic morphology of ensiferans is hitherto insufficiently studied, with publications that either give only a scarce description of the thoracic skeleton (Carpentier 1921; Richards 1955) or merely include a part of the thoracic musculature (Carpentier 1923; O'Brien & Field 2001). Only a single exceedingly detailed investigation of an ensiferan thorax provides descriptions of skeletal structures in addition to a complete portrayal of the muscular equipment, that of the house cricket *Acheta domesticus* (Voss 1905a,b,c,d, 1912).

With the emergence of innovative and non-invasive techniques, like confocal laser scanning microscopy (CLSM) and micro-computed tomography (µCT) (Fig. 5), the

investigation and documentation of morphological structures of animals became easier and in recent years astonishingly detailed (Metscher 2009; Friedrich *et al.* 2013). Established for insect morphology about 15 years ago (Hörnschemeyer *et al.* 2002), µCT is now one of the most commonly used techniques for studying the anatomy of small and medium sized insects (Friedrich *et al.* 2013). In contrast to a series of histological sections whose quality and alignment depends on the specific skills of the researcher µCT scans provide perfectly aligned image stacks that represent the ideal source for precise three-dimensional reconstructions of skeletal elements and musculature (Friedrich *et al.* 2013).

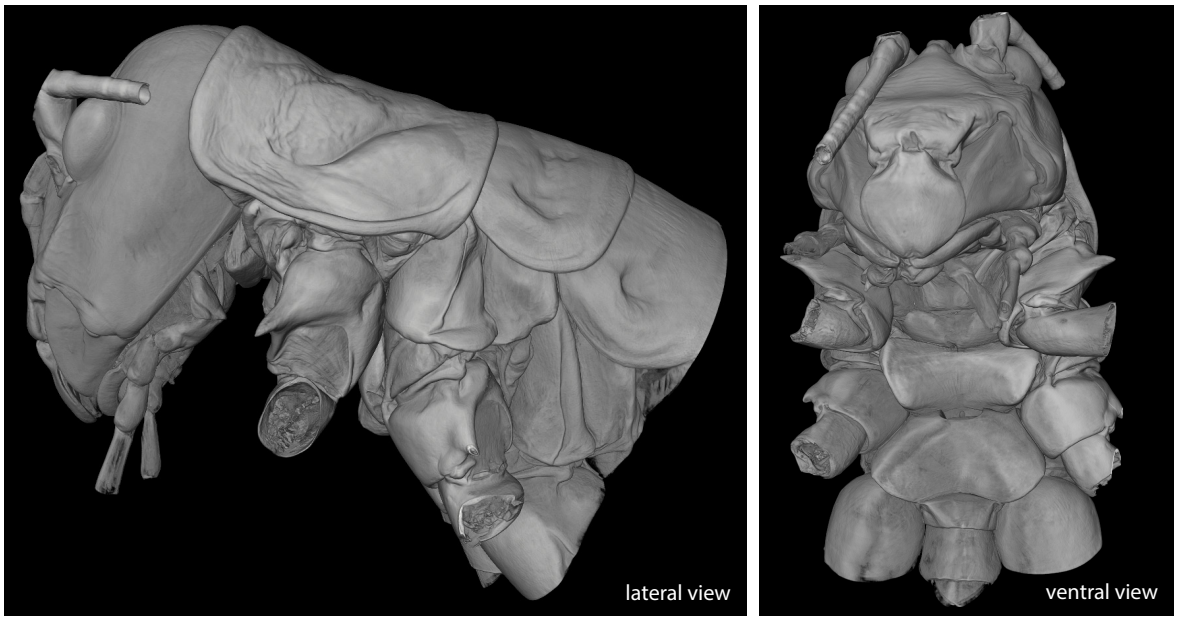


Figure 5. Head and thorax of *Hemideina crassidens* (Ensifera: Anostostomatidae) in lateral and ventral view. Volume rendering in Amira based on µ–computed tomography. According to the quality of the scan the three-dimensional view is exceedingly detailed. (Photo credit: Fanny Leubner).

Maki (1938) who studied the thoracic musculature in insects considered the musculature to be an important asset to determine the homology of the skeletal structures of insects. Aside from Maki, many others dealt with precise descriptions of the thoracic musculature in a number of different insect taxa (e.g. Snodgrass 1929; Rähle 1970; Bharadwaj & Chadwick 1974), but only few authors applied the nomenclature of preceding studies to their own results. As a consequence, a disastrous chaos was generated in homologizing and terming thoracic muscles of insects. To redeem and adjust this situation, Friedrich &

Beutel (2008) established a new and consistent nomenclature for the muscles potentially occurring in neopteran insects. According to its attachment sites, each muscle is now assigned to a certain muscle group, e.g. dorsoventral, ventral longitudinal or tergopleural, and to the specific thoracic segment, numbered consecutively and named after the skeletal elements on which it is attached, e.g. Idvm9 (*M. profurca-occipitalis*), IIvlm5 (*M. mesospina-metafurcalis*), IIItpm10 (*M. metepimero-subalaris*) (Fig. 6). Hence, the study of Friedrich & Beutel (2008) represents a fundamental contribution and the starting point for more comparable investigations of the musculature of insect thoraces allowing for facilitated descriptions and transparent presentations of novel results.

Based on the achievements of Friedrich & Beutel (2008), characters of the thoracic musculature of neopteran insects were extensively considered in a subsequent phylogenetic analysis of morphological characters of the thorax by Wipfler *et al.* (2015). Although Wipfler *et al.* (2015) answered some questions in regard of the evolution of the lower neopteran insects, like that concerning the monophyly of Polyneoptera or Xenonomia, the deeper nodes of the Polyneoptera remained completely unresolved. In terms of Orthoptera, Wipfler *et al.* (2015) only included data on the thoracic morphology

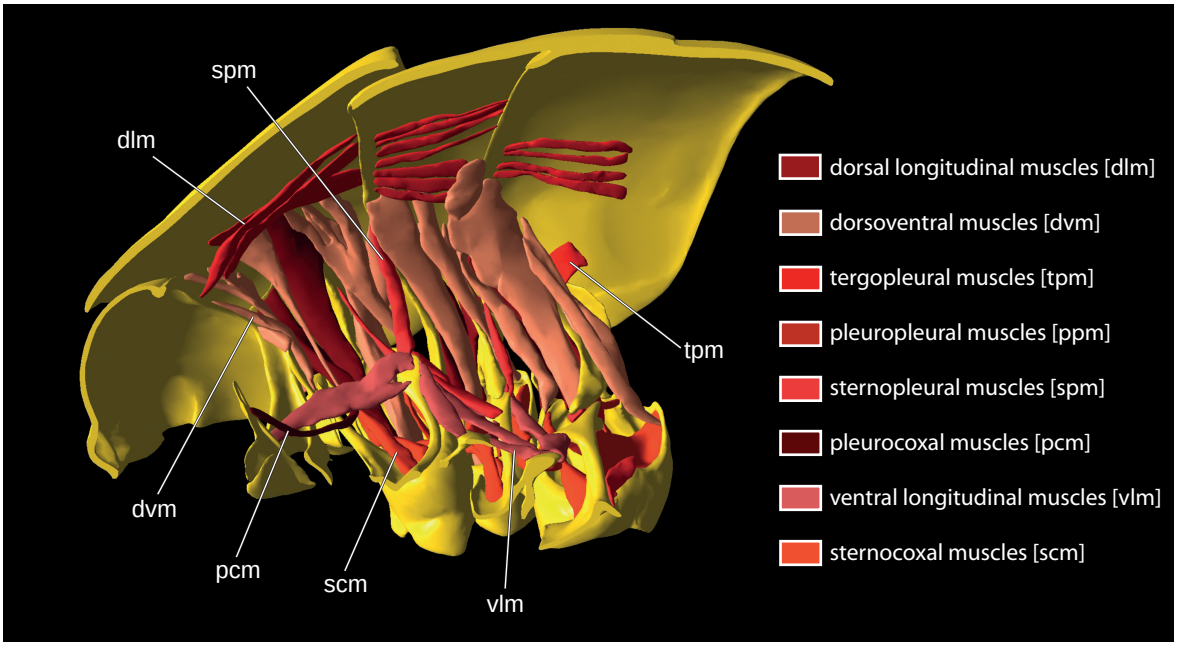


Figure 6. 3D-reconstruction of skeleton (yellow) and musculature (shades of red) in the thorax of T*roglophilus neglectus* (Ensifera: Rhaphidophoridae). Enumeration of all muscle groups presented in Friedrich & Beutel 2008 in addition to a selected example of each muscle group (except pleuropleural muscle). (Photo credit: Fanny Leubner).

of a single caeliferan representative, the grasshopper *Dissosteira thoracica* (Snodgrass 1929), and a single ensiferan representative, the house cricket *Acheta domesticus* (Voss 1905b,d). As outlined above, this taxon sampling is not an ideal choice to represent the Orthoptera for a phylogenetic analysis and does not at all reflect the taxonomic and morphological diversity of Orthoptera. The investigation of a wide spectrum of orthopteran representatives from both major subgroups is essential to reconstruct the groundplan morphology of the thoracic skeletomuscular system of Orthoptera.

Major aims

In total, four main aims will be addressed in the thesis:

(1) Morphology of the thoracic skeletomuscular system

A detailed examination and description of the morphology of the skeleton and musculature of the thorax in carefully chosen orthopteran key taxa is a major aim of the present thesis. 23 orthopteran representatives are studied, whereby data on the thoracic morphology available from previously published studies is also considered. In total, these represent 16 ensiferan representatives (14 investigated by myself, 2 described in literature) and 7 caeliferan representatives (2 investigated by myself, 5 described in literature). Thereby great emphasis is placed on a high-quality documentation using a broad spectrum of different morphological techniques. Based on this compiled information the groundplan morphology of this character system in Orthoptera is reconstructed (Chapter 3). Apart from these more general statements about the orthopteran thorax that of dune crickets (Ensifera: Schizodactylidae) is found to show several specific modifications strongly related to sandy and arid habitats (Chapter 2).

(2) Phylogeny of Ensifera and the systematic placement of Orthoptera among Polyneoptera

The main goal of this thesis is a reconstruction of the internal relationships of the long-horned grasshoppers (Ensifera). Furthermore, the systematic placement of Orthoptera among Polyneoptera is inferred based on the new data. In combination

with characters that were used in a previous cladistic analysis, numerous novel, largely orthopteran-specific characters are arranged in a data matrix and used for a formal cladistic analysis (Chapter 3).

(3) Secondary winglessness in Ensifera and other polyneopteran lineages

The comprehensive investigation of both winged and wingless ensiferan taxa will allow to draw conclusions about common morphological adaptations of the thorax that are related to secondary winglessness (Chapter 1, 2, 3). A comparison of the obtained data from winged and wingless orthopterans to the condition in other morphologically diverse polyneopteran taxa like Phasmatodea or Mantophasmatodea serves as the basis to determine whether transformations associated with wing loss follow the same pattern among Polyneoptera in general (Chapter 1). Based on the comparison of unrelated wingless ensiferan species I will outline morphological characteristics that indicate an independent loss of wings in those lineages (Chapter 1, 2).

(4) Implications for the evolution of bioacoustics within Ensifera

Based on the novel hypothesis of the internal ensiferan relationships, the origin of bioacoustics within the Ensifera is thoroughly discussed and preceding phylogenetic studies are critically reviewed. The literature dealing with bioacoustics of Ensifera, including morphological, neuroanatomical, physiological, behavioural and ecological studies, is concisely compiled and re-evaluated from an evolutionary point of view and in the light of my new results (Chapter 3).

References

Alexander, R. D. 1962. Evolutionary change in cricket acoustical communication. *Evolution*, **16**, 443–467.

Ander, K. 1939. Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria). *Opuscula Entomologica Supplementum II*, 1–306.

Beier, M. 1972. Saltatoria (Grillen und Heuschrecken). *In*: Helmcke, J. G., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–217.

Beutel, R. G. & Gorb, S. N. 2006. A revised interpretation of the evolution of attachment structures in Hexapoda with special emphasis on Mantophasmatodea. *Arthropod Systematics & Phylogeny*, **64**, 3–25.

Beutel, R. G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., Meier, R., Misof, B., Whiting, M. F. & Vilhelmsen, L. 2011. Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. *Cladistics*, **27**, 341–355.

Bharadwaj, R. K. & Chadwick, L. E. 1974. Postembryonic development of the cervico-thoracic skeleton of *Euborellia annulipes* (Lucas) (Dermaptera: Labiduridae). *Journal of Morphology*, **143**, 457–473.

Carpentier, F. 1921. Sur l'endosquelette prothoracique de *Gryllotalpa vulgaris*. *Bulletin de la Classe des Sciences, Académie Royale de Belgique*, **7**, 125–134.

Carpentier, F. 1923. Musculature et squelette chitineux: Recherches sur le comportement de la musculature des flancs dans les segments cryptopleuriens du thorax chez les orthoptères. *Mémoires de l'Académie royale de Belgique (2). Collection in -8°.*, **7 (3)**, 1–56.

Desutter-Grandcolas, L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta*, **32**, 525–561.

Eades, D. C., Otte, D., Cigliano, M. M. & Braun, H. 2015. Orthoptera Species File. Version 5.0/5.0. http://orthoptera.speciesfile.org. Accessed 10 Mar 2017.

Edmunds, M. 1974. *Defence in Animals: A Survey of Anti-Predator Defences*. Longman, New York, 357 pp pp.

Ewer, D. W. 1954. A Note on the comparative anatomy of the pterothorax of macropterous and brachypterous forms of the grasshopper *Zonocerus elegans* Thunb. *Journal of the Entomological Society of Southern Africa*, **17**, 237–240.

Friedrich, F. & Beutel, R. G. 2008. The thorax of *Zorotypus* (Hexapoda, Zoraptera) and a new nomenclature for the musculature of Neoptera. *Arthropod Structure & Development*, **37**, 29–54.

Friedrich, F., Matsumura, Y., Pohl, H., Bai, M., Hörnschemeyer, T. & Beutel, R. G. 2013. Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. *Entomological Science*, **17**, 1–24.

Grimaldi, D. & Engel, M. S. 2005. *Evolution of the Insects*. Cambridge University Press, New York, 720 pp.

Gwynne, D. T. 1995. Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research*, **4**, 203–218.

Gwynne, D. T. 2001. Entomological choristers: song and mate attraction. *In*: Alcock, J. (ed.) *Katydids and Bush-Crickets: Reproductive Behaviour and Evolution of the Tettigoniidae*. Cornell University Press, Ithaca, London, 89–121.

Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin, 370 pp.

Hörnschemeyer, T., Beutel, R. G. & Pasop, F. 2002. Head structures of *Priacma serrata* Leconte (Coleptera, Archostemata) inferred from X-ray tomography. *Journal of Morphology*, **252**, 298–314.

Irish, J. 1986. The species of *Comicus* Brunner v. Wattenwyl (Orthoptera: Schizodactylidae) with a discussion of their origin. *Navorsinge van die Nasionale Museum Bloemfontein*, **5**, 253–276.

Ishiwata, K., Sasaki, G., Ogawa, J., Miyata, T. & Su, Z. H. 2011. Phylogenetic relationships among insect orders based on three nuclear protein-coding gene sequences. *Molecular Phylogenetics and Evolution*, **58**, 169–180.

Jost, M. C. & Shaw, K. L. 2006. Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution*, **38**, 510–530.

Kevan, D. K. M. 1982. Orthoptera. *In*: Parker, S. P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill, Inc., New York, 352–379.

Kingsolver, J. G. 1985. Butterfly thermoregulation: organismic mechanisms and population consequences. *Journal of Research on the Lepidoptera*, **24**, 1–20.

Kjer, K. 2004. Aligned 18S and Insect Phylogeny. *Systematic Biology*, **53**, 506–514.

Klass, K.-D., Zompro, O., Kristensen, N. P. & Adis, J. 2002. Mantophasmatodea: a new insect order with extant members in the Afrotropics. *Science*, **296**, 1456–1459.

Kluge, N. J. 2016. Structure of ovipositors and cladoendesis of Saltatoria, or Orchesopia. *Entomological Review*, **96**, 1015–1040.

Korsunovskaya, O. S. 2008. Acoustic signals in katydids (Orthoptera, Tettigonidae). Communication 1. *Entomological Review*, **88**, 1032–1050.

Kristensen, N. P. 1991. Phylogeny of extant hexapods. *In*: *The Insects of Australia: A Textbook for Students and Research Workers*. 125–140.

Legendre, F., Robillard, T., Song, H., Whiting, M. F. & Desutter-Grandcolas, L. 2010. One hundred years of instability in ensiferan relationships. *Systematic Entomology*, **35**, 475–488.

Letsch, H. & Simon, S. 2013. Insect phylogenomics: new insights on the relationships of lower neopteran orders (Polyneoptera). *Systematic Entomology*, **38**, 783–793.

Maki, T. 1938. Studies on the thoracic musculature of insects. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University*, **24**, 1–343.

Metscher, B. D. 2009. MicroCT for comparative morphology: simple staining methods allow high-contrast 3D imaging of diverse non-mineralized animal tissues. *BMC Physiology*, **9**, 11.

Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, a., Mayer, C., Frandsen, P. B., Ware, J., Flouri, T., Beutel, R. G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, a. J., Aspock, U., Aspock, H., Bartel, D., Blanke, a., Berger, S., Bohm, a., Buckley, T. R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L. S., Kawahara, a. Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D. D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J. L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B. M., Schutte, K.,

Sekiya, K., Shimizu, S., Slipinski, a., Stamatakis, a., Song, W., Su, X., Szucsich, N. U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M. G., Wiegmann, B. M., Wilbrandt, J., Wipfler, B., Wong, T. K. F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D. K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Xu, X., Yang, H., Wang, J., Kjer, K. M. & Zhou, X. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.

Nickle, D. A. & Naskrecki, P. A. 1997. Recent developments in the systematics of Tettigoniidae and Gryllidae. *In*: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds) *The Bionomics of Grasshoppers, Katydids and Their Kin*. CAB International, Wallingford, New York, 41–58.

O'Brien, B. & Field, L. H. 2001. Morphology and anatomy of New Zealand wetas. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New York, 127–162.

Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research*, **1**, 25–49.

Ragge, D. R. 1955. *The Wing-Venation of the Orthoptera Saltatoria. With Notes on Dictyopteran Wing-Venation.* British Museum (Natural History), London, 1-159 pp.

Rähle, W. 1970. Untersuchungen am Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakow 1906 (Embioptera, Embiidae). *Zoologische Jahrbücher. Abteilung Anatomie und Ontogenie der Tiere*, **87**, 248–330.

Richards, A. M. 1955. The anatomy and morphology of the cave-orthopteran *Macropathus filifer* Walker, 1869. *Transactions of the Royal Society of New Zealand*, **83**, 405–452.

Robinson, D. J. & Hall, M. J. 2002. Sound signalling in Orthoptera. *In*: Evans, P. (ed.) *Advances in Insect Physiology*. Elsevier Ltd, 151–278.

Roff, D. A. 1994. The evolution of flightlessness: is history important? *Evolutionary Ecology*, **8**, 639–657.

Sharov, A. G. 1968. Phylogeny of the Orthopteroidea. *Transactions of the Institute of Paleontology. Academy of Sciences of the USSR.*, **118**, 1–251.

Snodgrass, R. E. 1929. The thoracic mechanism of a grasshopper, and its antecedents. *Smithsonian Miscellaneous Collections*, **82**, 1–111.

Snodgrass, R. E. 1935. *Principles of Insect Morphology*. 1993rd ed. McGraw-Hill, Inc., New York, London, 1-667 pp.

Song, H., Am, C., Marta, M., Desutter-, L., Heads, S. W., Huang, Y., Otte, D. & Whiting, M. F. 2015. 300 million years of diversification : elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics*, **31**, 621–651.

Song, N., Li, H., Song, F. & Cai, W. 2016. Molecular phylogeny of Polyneoptera (Insecta) inferred from expanded mitogenomic data. *Scientific Reports*, **6**, 36175.

Strauß, J., Lehmann, A. W. & Lehmann, G. U. C. 2014. Sensory evolution of hearing in tettigoniids with differing communication systems. *Journal of Evolutionary Biology*, **27**, 200–213.

Terry, M. D. & Whiting, M. F. 2005. Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics*, **21**, 240–257.

Trautwein, M. D., Wiegmann, B. M., Beutel, R., Kjer, K. M. & Yeates, D. K. 2012. Advances in insect phylogeny at the dawn of the postgenomic era. *Annual Review of Entomology*, **57**, 449–68.

Voss, F. 1905a. Über den Thorax von *Gryllus domesticus*. Dritter Teil. Die Mechanik. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 645–696.

Voss, F. 1905b. Über den Thorax von *Gryllus domesticus*. Erster Teil. Das Skelett. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (2)**, 268–514.

Voss, F. 1905c. Über den Thorax von *Gryllus domesticus*. Vierter Teil. Vergleich der Orthopteren, besonders des *Gryllus domesticus* mit den übrigen höheren Insektenordnungen. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 697–740.

Voss, F. 1905d. Über den Thorax von *Gryllus domesticus*. Zweiter Teil. Die Muskulatur. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 355–521.

Voss, F. 1912. Über den Thorax von *Gryllus domesticus*. Fünfter Teil. Die nachembryonale Metamorphose im ersten Stadium. *Zeitschrift für Wissenschaftliche Zoologie*, **101**, 579–682.

Wagner, D. L. & Liebherr, J. K. 1992. Flightlessness in Insects. *Trends in Ecology & Evolution*, **7**, 216–220.

Wang, Y., Engel, M. S., Rafael, J. A., Dang, K., Wu, H., Wang, Y., Xie, Q. & Bu, W. 2013. A unique box in 28S rRNA is shared by the enigmatic insect order Zoraptera and Dictyoptera. *PLoS ONE*, **8**, e53679.

Whitfield, J. B. & Kjer, K. M. 2008. Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annual review of entomology*, **53**, 449–472.

Wipfler, B., Klug, R., Ge, S.-Q., Bai, M., Göbbels, J., Yang, X.-K. & Hörnschemeyer, T. 2015. The thorax of Mantophasmatodea, the morphology of flightlessness, and the evolution of the neopteran insects. *Cladistics*, **31**, 50–70.

Yack, J. E. 2004. The structure and function of auditory chordotonal organs in insects. *Microscopy research and technique*, **63**, 315–337.

Yeates, D. K., Cameron, S. L. & Trautwein, M. 2012. A view from the edge of the forest: recent progress in understanding the relationships of the insect orders. *Australian Journal of Entomology*, **51**, 79–87.

Yoshizawa, K. 2011. Monophyletic Polyneoptera recovered by wing base structure. *Systematic Entomology*, **36**, 377–394.

Yoshizawa, K. & Johnson, K. P. 2005. Aligned 18S for Zoraptera (Insecta): Phylogenetic position and molecular evolution. *Molecular Phylogenetics and Evolution*, **37**, 572–580.

Zeuner, F. E. 1939. *Fossil Orthoptera Ensifera*. British Museum (Natural History), London, 1-321 pp.

Zhou, Z., Zhao, L., Liu, N., Guo, H., Guan, B., Di, J. & Shi, F. 2017. Towards a higher-level Ensifera phylogeny inferred from mitogenome sequences. *Molecular Phylogenetics and Evolution*, **108**, 22–33.

CHAPTER 1

The thorax of the cave cricket *Troglophilus neglectus*: anatomical adaptations in an ancient wingless insect lineage (Orthoptera: Rhaphidophoridae)

Fanny Leubner, Thomas Hörnschemeyer, Sven Bradler

published in:

Leubner, F., Hörnschemeyer, T., Bradler, S. 2016. The thorax of the cave cricket *Troglophilus neglectus*: anatomical adaptations in an ancient wingless insect lineage (Orthoptera: Rhaphidophoridae). *BMC Evolutionary Biology*, **16**, 39.

Abstract

Background: Secondary winglessness is a common phenomenon found among neopteran insects. With an estimated age of at least 140 million years, the cave crickets (Rhaphidophoridae) form the oldest exclusively wingless lineage within the long-horned grasshoppers (Ensifera). With respect to their morphology, cave crickets are generally considered to represent a `primitive' group of Ensifera, for which no apomorphic character has been reported so far.

Results: We present the first detailed investigation and description of the thoracic skeletal and muscular anatomy of the East Mediterranean cave cricket *Troglophilus neglectus* (Ensifera: Rhaphidophoridae). *T. neglectus* possesses sternopleural muscles that are not yet reported from other neopteran insects. Cave crickets in general exhibit some unique features with respect to their thoracic skeletal anatomy: an externally reduced prospinasternum, a narrow median sclerite situated between the meso- and metathorax, a star-shaped prospina, and a triramous metafurca. The thoracic muscle equipment of *T. neglectus* compared to that of the bush cricket *Conocephalus maculatus* (Ensifera: Tettigoniidae) and the house cricket *Acheta domesticus* (Ensifera: Gryllidae) reveals a number of potentially synapomorphic characters between these lineages.

Conclusions: Based on the observed morphology we favor a closer relationship of Rhaphidophoridae to Tettigoniidae rather than to Gryllidae. In addition, the comparison of the thoracic morphology of *T. neglectus* to that of other wingless Polyneoptera allows reliable conclusions about anatomical adaptations correlated with secondary winglessness. The anatomy in apterous Ensifera, viz. the reduction of discrete direct and indirect flight muscles as well as the strengthening of specific leg muscles, largely resembles the condition found in wingless stick insects (Euphasmatodea), but is strikingly different from that of other related wingless insects, e.g. heel walkers (Mantophasmatodea), ice crawlers (Grylloblattodea), and certain grasshoppers (Caelifera). The composition of direct flight muscles largely follows similar patterns in winged respectively wingless species within major polyneopteran lineages, but it is highly heterogeneous between those lineages.

Key words: Orthoptera, Ensifera, Rhaphidophoridae, winglessness, morphology, phylogeny

Introduction

The evolution of wings is considered to be a key innovation responsible for the unrivaled evolutionary success of insects, improving dispersal capability, predator avoidance, as well as the access to scattered food sources and mating partners (Wagner & Liebherr 1992). Beyond flight, wings can provide additional advantages, contributing to thermoregulation, defensive behavior and acoustic communication (Edmunds 1974; Kingsolver 1985; Robinson & Hall 2002). Yet, wing loss is a common phenomenon among pterygotes (Wagner & Liebherr 1992). In Ensifera (long-horned grasshoppers), one of the most species-rich lineages among the Polyneoptera, wings are often reduced to tiny remnants whose only purpose appears to be the production of sound (Beier 1972; Rentz 2010; Stumpner *et al.* 2015). Orthoptera in general have long been of interest to scientists studying intra-specific acoustic communication and hearing systems. Crickets (Gryllidae) and bush-crickets or katydids (Tettigoniidae) in particular are well known for their elaborate acoustic signaling via tegminal stridulation that is associated with mating and territorial behavior (Robinson & Hall 2002). In the last century, numerous biologists dedicated their research to bioacoustics and countless studies have been conducted illuminating the neuroanatomical (Strauß & Lakes-Harlan 2008, 2009), behavioral (Otte 1992) and evolutionary (Field 1993; Strauß & Stumpner 2015) background of ensiferan bioacoustics. Some ensiferan taxa have completely reduced their wings, nevertheless. To understand the evolution of bioacoustics within the Ensifera special attention was paid to these wingless and deaf taxa, such as the Rhaphidophoridae, commonly known as camel and cave crickets. The neuroanatomy of their chordotonal organs (Strauß & Stumpner 2015) as well as their vibratory communication through low frequencies (Stritih & Čokl 2012) is assumed to reflect the ancestral condition of bioacoustics within the Ensifera. Also in regard of their overall morphology, cave crickets are considered a ´primitive` lineage among Ensifera preserving several characters in their plesiomorphic state, e.g. the morphology of the ovipositor, the absence of tarsal pulvilli and the absence of posterofurcal connectives in the thorax (Ander 1939). With about 550 described species, these insects form an ecologically specialized group mainly adapted to cave life (Beier 1972). Rhaphidophoridae has a disjunct geographical distribution restricted to the temperate areas of the Northern and Southern hemispheres as reflected by their phylogeny (Hubbell & Norton 1978). Rhaphidophoridae

comprises two major groups: Rhaphidophorinae, distributed in Eurasia and North America, and Macropthinae that is restricted to South Africa, South America and New Zealand (Karny 1934; Allegrucci *et al.* 2010). Although the monophyly of Rhaphidophoridae is well supported in molecular analyses (Rowell & Flook 1998; Jost & Shaw 2006; Legendre *et al.* 2010; Song *et al.* 2015), cladistic analyses of morphological characters indeed did not identify any supporting apomorphy for this clade (Gwynne 1995; Desutter-Grandcolas 2003). The species *Troglophilus neglectus* investigated in this study appears to branch off from a basal node, forming the sister taxon to the remaining Rhaphidophoridae (Song *et al.* 2015). In this respect, *T. neglectus* likely retains characters from the last common ancestor of Rhaphidophoridae and can be considered representative for this taxon in general.

Numerous hennigian (mental) and cladistic studies of Ensifera including Rhaphidophoridae have led to competing hypotheses with respect to the relative positions of the two most species-rich groups within the Ensifera, the true crickets (Gryllidae) and the bush-crickets (Tettigoniidae) (Additional file 1). Traditionally, ensiferan taxonomy is based on the morphology of wings and wing venation in particular. Interestingly, the phylogenetic hypotheses based on this specific character complex differ remarkably. Following the classification scheme of Handlirsch (1929), Zeuner (1939) proposed a closer relationship of crickets ('Grylloidea' therein) and bush-crickets ('Tettigoniidae' therein) and considered both taxa as having evolved from different fossil representatives of the Prophalangopsidae. He considered the tegminal stridulation and its specific wing morphology as an apomorphic character in the last common ancestor of crickets and bush-crickets. On the other hand, Karny (1921, 1937) and Sharov (1968) shared the opinion that the true crickets and relatives (mole crickets, Gryllotalpidae, and antloving crickets, Myrmecophilinae) originated from the gryllacridids (including Rhaphidophoridae), whereas the bush-crickets (Tettigoniidae) were assumed to form an independent lineage within the Ensifera. However, the majority of hennigian and cladistic morphological studies (Ander 1939; Gorochov 1995; Gwynne 1995; Desutter-Grandcolas 2003) as well as phylogenetic analyses based on molecular data (Flook *et al.* 1999; Fenn *et al.* 2008; Sheffield *et al.* 2010; Zhang *et al.* 2013; Zhou *et al.* 2014; Song *et al.* 2015) propose a division of the Ensifera in two major groups: the "grylloid" clade, including true crickets (Gryllidae), mole crickets (Gryllotalpidae) and antloving crickets (Myrmecophilinae), and a "tettigonioid" clade, comprising the bush-crickets (Tettigoniidae), cave crickets (Rhaphidophoridae), wetas (Anostostomatidae),

Jerusalem crickets (Stenopelmatidae) and raspy crickets (Gryllacrididae). Dune crickets (Schizodactylidae) are assigned to either of these two clades according to different authors (Gwynne 1995; Desutter-Grandcolas 2003).

While studies solely based on molecular data may provide a robust phylogenetic framework for any given organismic group, comparative morphological research is essential for interpreting evolutionary scenarios (Giribet 2015) and tracing functional transformations and adaptations (Friedrich *et al.* 2013). In particular, the morphology of insect thoraces has repeatedly played a substantial role in understanding the systematics and evolution of certain insect groups (Friedrich & Beutel 2008; Friedrich *et al.* 2009; Koeth *et al.* 2012; Büsse & Hörnschemeyer 2013). In Ensifera this character complex is hitherto insufficiently studied, with publications that either give only a scarce description of the thoracic skeleton and/or merely include a part of the thoracic musculature. Very few detailed investigations of ensiferan thoraces provide characterizations of skeletal structures in addition to a complete description of the muscular equipment. These studies only consider representatives of the most species-rich ensiferan lineages: Voss (1905a,b; 1912a,b) gives an exceedingly detailed description of the thorax of the house cricket *Acheta domesticus* (Gryllidae), whereas Maki (Maki 1938) provides the only existing description of the thoracic musculature of a bush-cricket, *Conocephalus maculatus* (Tettigoniidae). Studies focusing on the thoracic morphology of Rhaphidophoridae are scarce. Carpentier (1921a) gives a brief description of the thoracic skeleton of the greenhouse stone cricket *Diestrammena asynamora* (Rhaphidophorinae) in addition to a study of its pleural musculature (Carpentier 1923). Furthermore, Richards (1955) presents a fragmentary description of the thoracic morphology of *Macropathus filifer*, a rhaphidophoridean species belonging to the southern group Macropathinae.

Here we present a detailed description of the skeletal structures and the muscular equipment of the thorax of the East Mediterranean cave cricket *Troglophilus neglectus* (Rhaphidophorinae). The thoracic morphology of *T. neglectus* is compared to the conditions found in other representatives of Orthoptera in order to detect possible apomorphic traits of Rhaphidophoridae. Furthermore, the investigated character complex is evaluated in the context of its phylogenetic information content, and potential synapomorphies of the competing phylogenetic hypotheses of ensiferan relationships are discussed. Moreover, the general nomenclature recently proposed for thoracic musculature of Neoptera

(Friedrich & Beutel 2008) is critically revisited in light of our results. It is evident that within the Neoptera wings were lost several times in evolution and was a step-like process with numerous morphological transformations in each lineage. Therefore, our observations are compared to the thoracic morphology of other wingless polyneopteran representatives, such as the Zoraptera (Friedrich & Beutel 2008), Mantophasmatodea (Wipfler *et al.* 2015) or Phasmatodea (Klug 2008) in order to compile common adaptations of the thoracic skeletal and muscular system related to secondary winglessness. Based on our novel anatomical data we will provide a detailed description of the consequences of wing loss on the functional anatomy of insect thoraces and thoroughly address the question whether these transformations follow a similar pattern.

Material & Methods

Specimens

The specimens investigated in this study were collected in Brje pri Komnu, Slovenia, in July 2008 and identified as *Troglophilus* (*Paratroglophilus*) *neglectus* Krauss, 1879 (Stumpner *et al.* 2015). All specimens were preserved in 70% ethanol. For the sake of consistency in subsequent comparative studies, all investigated specimens are female adults. In total, four individuals were investigated using the following different methods.

High-resolution photography

Three specimens were used to investigate and illustrate the thoracic skeleton. One complete and undamaged specimen was dehydrated in a graded ethanol series and critical-point dried (Balzer CPD 030) to visualize the outer lateral and dorsal view. Another specimen was sagitally cut and macerated in 5% KOH (1 hour in a heating cabinet with 60°C) and likewise dried at critical point. Critical-point drying was applied to improve the contrast of the thoracic sclerites against the membranous areas and to visualize the sclerites in more detail. One specimen was fixed in a ventrally overstretched position to expose the neck region and subsequently dried using the HMDS (Hexamethyldisilazane, Carl Roth GmbH & Co KG, item number 3840.2) procedure (Friedrich *et al.* 2013). Photographs of the HMDS-dried specimen were taken using a digital camera (OLYMPUS Pen E-P2) mounted on a

stereomicroscope ZEISS Stemi SV11. The critical-point dried specimens were photographed with a CANON EOS 550D equipped with a macro lens (100 mm) and a ring flash (METZ 15 MS-1). The overall sharp images are composed of image stacks edited in Helicon Focus® (Helicon Soft) and Adobe Photoshop® CS3.

Synchrotron radiation micro computer tomography (SRμCT) and 3D-reconstruction

In order to investigate the thoracic musculature, one specimen was dehydrated in a graded ethanol series, critical-point dried (Balzer CPD 030) and mounted on a specimen holder (aluminium stub). The scan was performed at the synchrotron radiation facility BESSY II (Berlin, Germany). The three-dimensional model of the thorax was created using AMIRA®5.4.3 and Autodesk Maya® 2013. Rendered images were edited using Adobe Illustrator® CS3.

Terminology

The terminology of the thoracic skeleton largely follows Snodgrass (1935) and Friedrich & Beutel (2008). Terms used by authors of ensiferan-specific literature (e.g. Voss 1905a; Ander 1939) are mentioned in the case of inconsistency. The thoracic musculature of *Troglophilus* (*Paratroglophilus*) *neglectus* is described and muscles are numbered consecutively. We homologize the observed muscles in *Troglophilus*, in addition to that of two other ensiferans, *Conocephalus maculatus* (Maki 1938) (*Xiphidion maculatum* therein) and *Acheta domesticus* (Voss 1905b) (*Gryllus domesticus* therein) with the muscles described following the nomenclature of Friedrich & Beutel (2008) for neopteran insects, allowing for comparison to studies of other authors. The distinctive set of thoracic muscles found in *Troglophilus* is compared with the condition in other polyneopteran taxa, i.e. two grasshoppers (Caelifera), *Locusta migratoria migratorioides* (Maki 1938) (*Locusta migratoria manilensis* therein) and *Atractomorpha sinensis* (Maki 1938) (*Atractomorpha ambigua* therein), two stick insects (Phasmatodea), *Carausius morosus* (Jeziorski 1918) (*Dixippus morosus* therein) and *Megacrania tsudai* (Maki 1935), and one heelwalker (Mantophasmatodea), *Austrophasma caledonensis* (Wipfler *et al.* 2015). The current taxonomy of the examined species follows Eades et al. (Eades *et al.* 2015) and Brock (Brock 2014).

Results

Skeleton

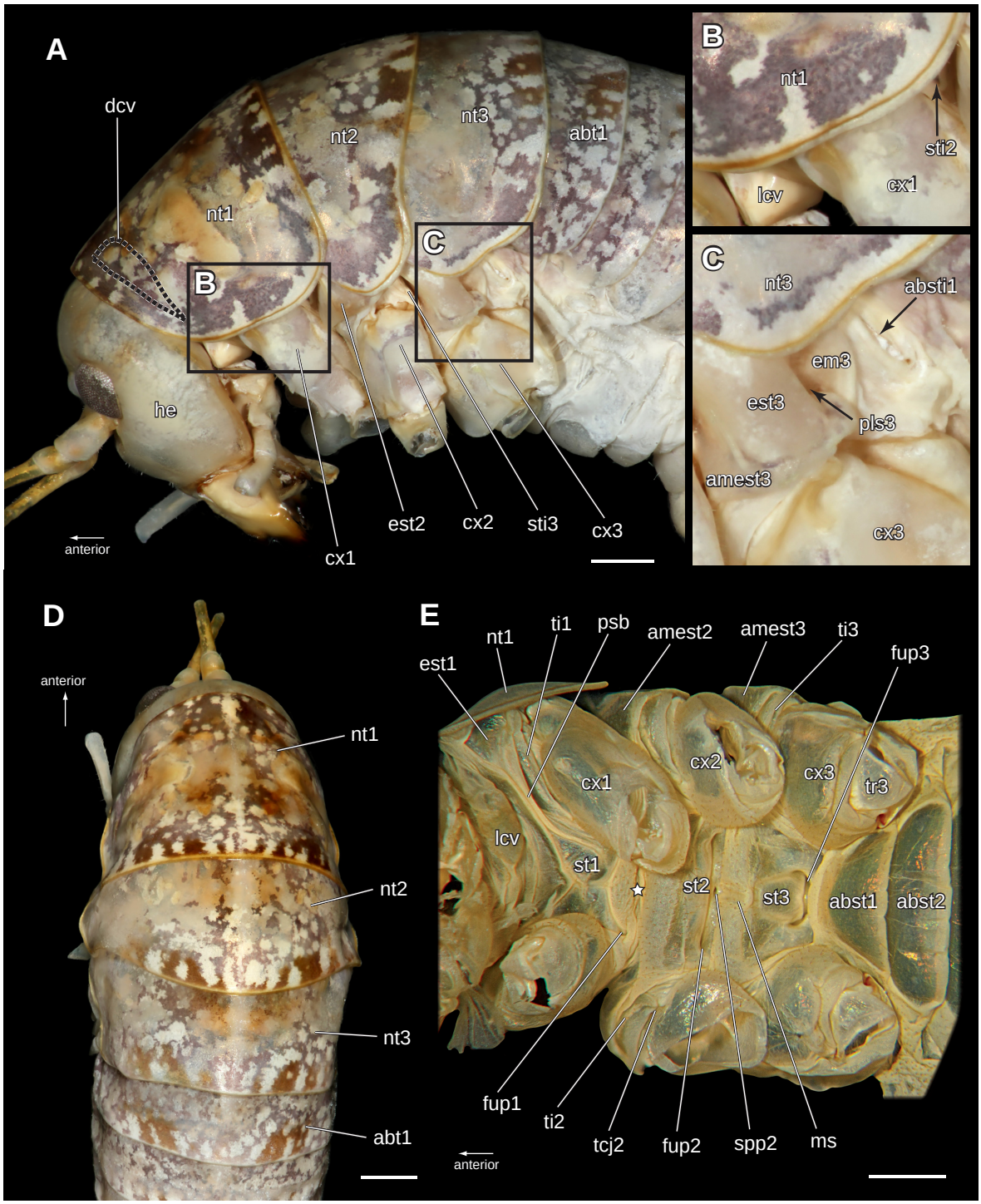
The thorax of *T. neglectus* comprises approximately two thirds of the total body length and is strongly curved downwards with the dorsal side nearly two times longer than the ventral side. The sclerites are colored light brown, speckled with dark reddish brown. All thoracic terga are ventrally elongated and saddle-shaped, masking great parts of the thoracic pleura in a lateral view (Fig. 1A). Wings and wing base sclerites are lacking. The phragmata are weakly developed and function as attachment points for the poorly developed dorsal longitudinal muscles. Ventrally, the anterior parts of the sterna, the membranous areas between these sclerites, and the inner surfaces of the coxae are covered by numerous setae (Fig. 1E).

Prothorax

An extensive cervical membrane connects the thorax to the head capsule. Several sclerites stabilize the cervical membrane and function as articulated connections between the head and the prothorax. The single lateral cervical sclerite **lcv** on each side consists of two connected parts being arcuate towards each other on the ventral side (Figs. 1A, B; 2B, D). The anterior part is of nearly triangular shape, the longest edge projecting medially. The anterior part extends dorsally to a slender, well sclerotized process, which articulates laterally with the occipital rim **ocr** of the head (Fig. 2D). The posterior part of the lateral cervical sclerite is triangular and its dorsal part articulates with the pleurosternal bridge **psb** of the prothorax (Fig. 2D).

Figure 1. Exterior view of the thoracic skeleton of *Troglophilus neglectus*, legs removed (see opposite page). (A) Lateral view of left body side. The position of the dorsal cervical sclerite (dcv) is marked by the dashed line. (B), (C) Enlarged details of the cervical and thoracic pleural region as indicated in (A). (D) Dorsal view. (E) Ventral view. The white asterisk marks the invagination point of the prospina. The specimen figured in (A)–(D) is critical-point dried; the specimen depicted in (E) is dried with HMDS in an overstretched position to provide visibility of the cervical region. Abbreviations: *abst1/2* first/second abdominal sternum, *absti1* first abdominal stigma, *abt1* first abdominal tergum, *amest2/3* anterior margin of mes-/metepisternum, *cx1/2/3* pro-/meso-/metacoxa, *dcv* dorsal cervical sclerite, *em3* metepimeron, *est1/2/3* pro-/meso-/metepisternum, *fup1/2/3* furcal pit of pro-/meso-/metasternum, *lcv* lateral cervical sclerite, *ms*, median sclerite, *nt1/2/3* pro-/meso-/metanotum, *pls3* metathoracic pleural suture, *psb* pleuro-sternal bridge, *spp2* mesospinal pit, *st1/2/3* pro-/meso-/metasternum, *sti2/3* meso-/metathoracal stigma, *tcj2* trochantino-coxal joint of mesothorax, *ti1/2/3* pro-/meso-/metatrochantin, *tr3* metatrochanter. Scale bars: 1 mm.

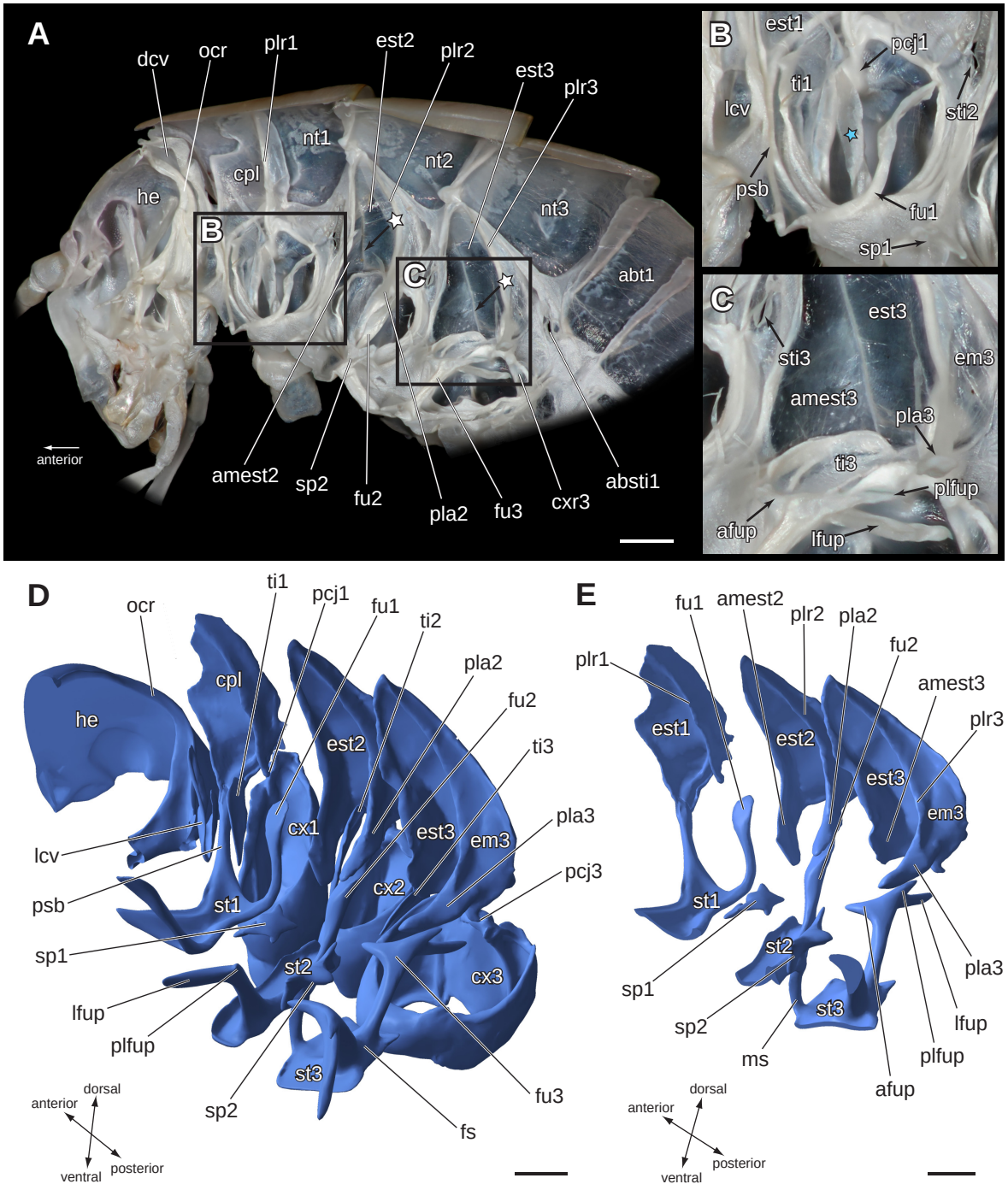
The unpaired dorsal cervical sclerite **dcv** is weakly sclerotized and situated in the upper half of the cervical membrane (Figs. 1A; 2A). This sclerite has a clip-like appearance reminiscent of a headband, widened at the dorsal side, narrowing strongly towards the ventral side. It is completely covered by the saddle-shaped pronotum **nt1** (Fig. 1A) and only visible when the neck membrane is overstretched. The pronotum has a smooth surface without distinct



ridges or grooves. It is laterally extended and bent ventrally, covering most of the propleura. The posterior part of the pronotum overlaps the mesonotum **nt2** (Fig. 1A, D). At the ventral side, the pronotum is continuous with an inward directed membranous fold that is connected to the exterior face in the lower third of the cryptopleura **cpl** (*Pleurallamelle* in Voss 1905a). The cryptopleura is sail-shaped (Fig. 2A, D). The pleural suture divides the cryptopleura in an anterior episternum and a posterior epimeron. The inner propleural ridge **plr1** is well developed and forms the pleurocoxal articulation **pcj1** at its ventral tip with the lateral procoxal rim (Fig. 2). The proepisternum **est1** is distinctly larger than the narrow proepimeron, which is merely the posterior part of the pleural ridge. The upper part of the proepisternum is thin and broadened and serves as an attachment point for several pleurocoxal muscles (m14–m16; see Fig. 3D, E). The lower part of the proepisternum **est1** bears a vesicular protrusion (Fig. 2B), which is the only visible part of the cryptopleura from an outer ventrolateral view. The anterior ventral angle of the proepisternum is continuous through the pleurosternal bridge **psb** (*precoxal bridge* in Snodgrass 1929; *Coxosternum* in Voss 1905a) with the anterior lateral angle of the prosternum **st1** (Fig. 2). The prosternum is nearly rectangular, but it shows a constriction along the ventromedian axis (Figs. 1E; 2D). The prosternal margins appear as strongly sclerotized ridges. The lateral and posterior ridges converge at each posterolateral corner of the prosternum and bear the inner profurca **fu1** (Fig. 2B, D). The profurca consists of a slender stem, which extends to a laterally orientated, shovel-shaped profurcal arm. From the exterior no spinasternum is recognizable (Fig. 1E). However, the internally located prospina **sp1** is well developed. It has a star-like shape from a top view with paired anterolateral and posterolateral processes and an unpaired anterior

Figure 2. Interior view of the thoracic skeleton of *T. neglectus* (see opposite page). (A)–(C) Photographs, (D)–(E) Three-dimensional reconstruction of skeletal elements of right half of thorax based on SRμCT-sections. (A) Lateral view of right body half. White asterisks mark the strongly sclerotized edge between episternum est and its anterior margin amest. (B) Detail of prothoracic sternopleural region. The blue asterisk marks the tendon of muscle 11 (Idvm19). (C) Detail of metathoracic sternopleural region. (D) Inner posterolateral view, terga removed. (E) Inner posterolateral view, showing sternal and pleural skeletal elements, only. Abbreviations: *absti1* first abdominal stigma, *abt1* first abdominal tergum, *afup* anterior furcal process, *amest2/3* anterior margin of mes-/metepisternum, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *cxr3* metacoxal rim, *dcv* dorsal cervical sclerite, *em3* metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lcv* lateral cervical sclerite, *lfup* lateral furcal process, *ms* median sclerite, *nt1/2/3* pro-/meso-/metanotum, *ocr* occipital rim, *pcj1/2/3* pleurocoxal joint of pro-/meso-/metathorax, *pla2/3* meso-/metathoracic pleural arm, *plfup* posterolateral furcal process, *plr1/2/3* pro-/meso-/metathoracic pleural ridge, *psb* pleurosternal bridge, *sp1/2* pro-/mesospina, *st1/2/3* pro-/meso-/metasternum, *sti2/3* meso-/metathoracal stigma, *ti1 /2/3* pro-/meso-/metatrochantin. Scale bars: 1 mm.

process (Fig. 2E). The feather-shaped prothoracic trochantin **ti1** is exposed in front of the coxal rim. Its ventral tip articulates with the anteromedian part of the procoxa **cx1** (Fig. 2B, D). Two sternocoxal muscles (m27, m28) are attached to inner processes of the large oval procoxal rim, one mediad and one laterad (Fig. 4).



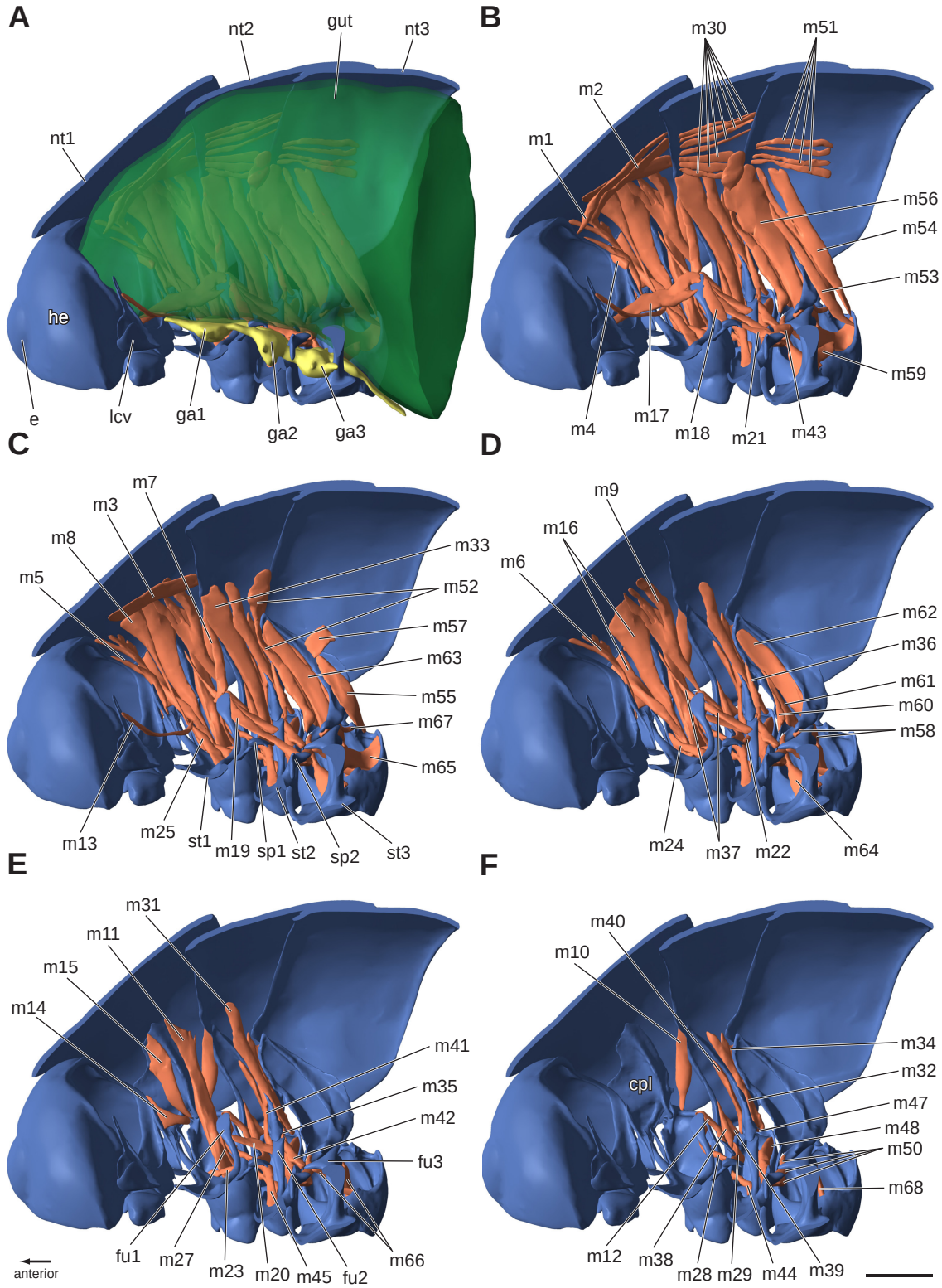


Figure 3. Thoracic skeletomuscular system of *T. neglectus*. Three-dimensional reconstruction of right half of thorax based on SRμCT-sections. Muscles: red; skeleton: blue; digestive tract: green; nervous system: yellow. Virtual dissection (A–F). Abbreviations: *cpl* cryptopleura, *e* compound eye, *he* head, *lcv* lateral cervical sclerite, *nt1/2/3* pro-/meso-/metanotum, *fu1/2/3* pro-/meso-/metafurca, *ga1/2/3* pro-/meso-/metathoracic ganglion, *sp1/2* pro-/meso-spina, *st1/2/3* pro-/meso-/metasternum. For muscle terminology see text and Table 1. Scale bar: 1 mm.

Mesothorax

The meso- and metathorax are almost identical in size. Like the pronotum **nt1**, also the pterothoracic nota **nt2/nt3** show no external or internal sculpturing and are ventrally elongated covering the most part of the pterothoracic pleura (Fig. 1A, D). The mesopleura has a triangular form tapering at the dorsal side. The mesepisternum **est2** is much broader than the epimeron **em2** (Fig. 2). The mesepisternum is folded inwards at the anterior edge projecting into a median direction in an obtuse angle. This inwardly folded part of the episternum is referred to as anterior margin **amest2** (Fig. 2A, E) and serves as an attachment area for several muscles (m38, m39).

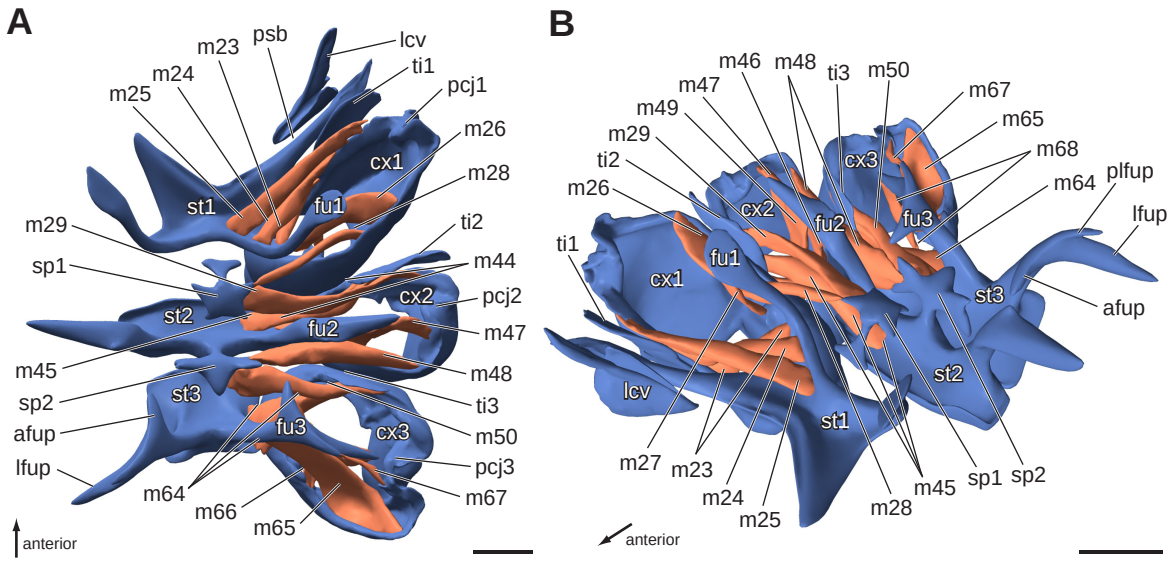


Figure 4. Sternocoxal muscles (scm) of *T. neglectus*. Three-dimensional reconstruction based on SRμCT-sections. (A) Dorsal view. (B) Anterolateral view. Abbreviations: *afup* anterior furcal process, *cx1/2/3* pro-/meso-/ metacoxa, *fu1/2/3* pro-/meso-/metafurca, *lcv* lateral cervical sclerite, *lfup* lateral furcal process, *pcj1/2/3* pleurocoxal joint of pro-/meso-/metathorax, *plfup* posterolateral furcal process, *psb* pleurosternal bridge, *sp1/2* pro-/mesospina, *st1/2/3* pro-/meso-/metasternum, *ti1/2/3* pro-/meso-/metathoracic trochantin. For muscle terminology see text and Table 1. Scale bars: 500 μm.

The anterior edge of the mesepisternum, connecting the episternum with its anterior margin, is forming a strongly sclerotized ridge (marked by white asterisks in Fig. 2A). The anterior margin of the mesepisternum extends medially onto the level of the trochantinocoxal joint. A massive and long pleural arm **pla2** protrudes from the straight mesopleural ridge **plr2** (Fig. 2D, E). A sclerotized bridge between the pleura and the sternum is absent in the mesothorax.

The mesosternum **st2** has a trapezoid shape, the longer edge orientated towards the head. The margins of the mesosternum are relatively indistinct because it is not delimited by strongly marked ridges as is the prosternum. The furcal pit **fup2** and the spinal pit **spp2** are located along a longitudinal groove at the posterior margin of the mesosternum **st2** (Fig. 1E). The mesothoracic furca **fu2** has a long lateral process **lfup** and a short posterolateral process **plfup** (Fig. 2D). The form of the mesothoracic spina **sp2** is reminiscent of a butterfly with expanded wings consisting of paired dorsolateral and ventrolateral processes and an unpaired posterodorsal one (Figs. 2D, E; 4B). The mesospina is situated slightly posterior from and between the laterally exposed furcae. A distinct and isolated spinasternum is absent. Directly posterior to the mesospinal pit **spp2**, the sterna of the meso- and metathorax are flexibly connected by a lathy median sclerite **ms** (*Mediansklerit* in Ander 1939), Fig. 1E). The slender and feather-shaped mesothoracic trochantin **ti2** articulates anteroventrally with the coxa **cx2**.

Metathorax

In general, the morphology of the tergum and pleuron of the pterothoracic segments is similar. Compared to the mesopleuron, the anterior margin of the metepisternum **amest3** has a broader basis (Fig. 2C, E). Main differences in the morphology of the pterothoracic segments are related to the sterna. The sternum of the metathorax **st3** is trapezoid in shape. It is narrower but longer than the mesosternum (Fig. 1E). The posteromedian located furcal pit **fup3** is more or less U-shaped. Internally, the metafurcae **fu3** of each body side are joined in a short common stem **fs** (Fig. 2A, D). The laterally projecting metafurcal arms bear a lateral process **lfup**, a posterolateral process **plfup**, and an anterior process **afup** (Fig. 2C, E). A spina is absent in the metathorax.

Thoracic musculature of T. neglectus *and its homologization with thoracic muscles of other Neoptera*

The thoracic muscles of *T. neglectus* are illustrated in figures 3 and 4. The detailed description of these muscles is provided in table 1 containing origin, insertion and specific characteristics. In addition, table 1 provides a hypothesis for the homology of the muscles of *T. neglectus* with the muscles generally reported from neopteran insects according to the nomenclature of Friedrich & Beutel (2008). In general, a thoracic muscle is treated

as an individual unit when both origin and insertion and, in addition, the function of this specific muscle are different from other thoracic muscles found in the thorax. Muscles that possess several bundles are characterized through differently originating muscle parts running together in one tendon at a common insertion point (e.g. m16). On the other hand, muscles can run parallel but their origin and insertion is clearly separated nontheless having the same function. These muscles are treated as derivatives of a single muscle (e.g. m44, m45).

Table 1. List of thoracic muscles of the cave cricket *Troglophilus neglectus*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the article. Furthermore, homologization (Hom*) according to the nomenclature after (Friedrich & Beutel 2008) is provided.

Present study	Hom*	Origin	Insertion	Remarks	Figure
Prothorax					
dorsal longitudinal muscles					
m1	Idlm1	median region of prophragma	dorsal area of occipital rim (close to m2)		3B
m2	Idlm3	prophragma (between m1 and m3)	cervical membrane		3B
m3	Idlm5	anterior dorsomedial pronotal region	lateral region of prophragma	flattened, broad	3C
dorsoventral muscles					
m4	Idvm1	anterior process of lateral cervical sclerite	dorsolateral area of occipital rim (ventrad of m5)	short, thin	3B
m5	Idvm2+3	posterior on inner face of lateral cervical sclerite	dorsolateral area of occipital rim	long, slim	3C
m6	Idvm5	anterior part of pronotum (near m8)	posterior part of lateral cervical sclerites near cervicopleural articulation point	fan-shaped, long thin tendon	3D
m7	Idvm10	laterodorsal face of profural arm	ventrolateral area of prophragma		3C
m8	Idvm13	dorsolateral area of pronotum (above cryptopleura)	trochantin	long thin tendon	3C
m9	Idvm16?	lateral region of pronotum (posterior to cryptopleura)	posterolateral procoxal rim (close to m26)	strongly developed	3D
m10	Idvm18	posterolateral region of pronotum	posterolateral procoxal rim (close to pleurocoxal joint)		3F
m11	Idvm19	lateral area of pronotum (posterior to cryptopleura, beneath m9)	trochanter (with m16)	strongly developed	3E
sternopleural muscles					
m12	Ispm5?	distal on ventral surface of profurcal arm	ventral part of anterior margin of mesepisternum	slender	3F

Table 1. List of thoracic muscles of the cave cricket *Troglophilus neglectus*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the article. Furthermore, homologization (Hom*) according to the nomenclature after (Friedrich & Beutel 2008) is provided. *(continued)*

Present study	Hom*	Origin	Insertion	Remarks	Figure
pleurocoxal muscles					
m13	Ipcm2	anterior procoxal rim	posterior face of anterior process of lateral cervical sclerite of opposite site (near cervicooccipital articulation point)	slender	3C
m14	Ipcm4	anterior margin of cryptopleura	anterior procoxal rim (close to m15)		3E
m15	Ipcm5	anterodorsal area of cryptopleura	anterior procoxal rim (close to pleurocoxal joint)		3E
m16	Ipcm8	anterolateral and anterodorsal area of cryptopleura	trochanter (with m11)	largest muscle in prothorax, strongly developed, 2 bundles	3D
ventral longitudinal muscles					
m17	Ivlm3	dorsal surface of profurcal arm	ventral area of occipital rim	strongly developed	3B
m18	Ivlm4	posterior margin of profurcal arm	anterolateral process of prospina		3B
m19	Ivlm6	posterior margin of profurcal arm (beneath m18)	anterior face of dorsolateral process of mesospina		3C
m20	Ivlm7	proximal at posterior margin of profurcal arm	anterior margin of mesofurcal arm		3E
m21	Ivlm8	posterior margin of posterolateral process of prospina	dorsal face of mesospina		3B
m22	Ivlm9	posterolateral process of prospina	anterior margin of mesofurcal arm (proximad of m20 & m37)		3D
sternocoxal muscles					
m23	Iscm1-1	lateral face of profurcal stem	anteromediad procoxal rim (mediad of m24)		3E, 4A, 4B
m24	Iscm1-2	anterolateral face of profurcal stem	anterior procoxal rim (close to trochantinocoxal articulation point)		3D, 4A, 4B
m25	Iscm1-3	medial face of profurcal stem and adjacent prosternum	anterior procoxal rim (laterad of m24)		3C, 4A, 4B
m26	Iscm2	ventral face of profurcal arm	posterolateral procoxal rim		4A, 4B
m27	Iscm3	distal on ventral face of profurcal arm	posterior procoxal rim on inner median process	slender	3E, 4B
m28	Iscm5	tip of anterolateral prospinal process	posterior procoxal rim on inner lateral process		3F, 4A, 4B
m29	Iscm7	lateral processi of prospina	anterior mesocoxal rim		3F, 4A, 4B

Table 1. List of thoracic muscles of the cave cricket *Troglophilus neglectus*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the article. Furthermore, homologization (Hom*) according to the nomenclature after (Friedrich & Beutel 2008) is provided. *(continued)*

Present study	Hom*	Origin	Insertion	Remarks	Figure
Mesothorax					
dorsal longitudinal muscles					
m30	IIdlm1	median region of prophragma	median region of mesophragma	several indistinct bundles as thin muscle layer	3B
dorsoventral muscles					
m31	IIdvm4+5	central region of mesonotum	posterior mesocoxal rim	two independent muscles sharing one insertion point	3E
m32	IIdvm6	dorsal edge of mesepimeron (ventrad of m31)	posterior mesocoxal rim (close to pleurocoxal joint)		3F
m33	IIdvm7	anterior region of mesonotum	trochanter (with m41 & m49)	largest muscle in mesothorax	3C
tergopleural muscles					
m34	IItpm10	epimeral face of mesopleural ridge	lateral region of mesonotum (ventrad of m32)	flattened	3F
sternopleural muscles					
m35	IIspm2	dorsal surface of mesofurca	ventral surface of mesopleural arm	poorly developed	3E
m36	IIspm6	posterior mesofurcal process	anterodorsal margin of metepisternum		3D
m37	IIspm?	anterior margin of mesofurcal arm (close to m20)	epimeral face of propleural ridge on cryptopleura	long thin tendon	3D
pleurocoxal muscles					
m38	IIpcm1	anterior margin of mesepisternum (close to m39)	trochantin		3F
m39	IIpcm2	inner anterodorsal part of anterior margin of mesepisternum	anterior mesocoxal rim		3F
m40	IIpcm3+4	episternal face of mesopleural ridge, few fibers from mesopleural arm	anterolateral mesocoxal rim	long, slender	3F
m41	IIpcm5	episternal face of mesopleural ridge and mesopleural arm	trochanter (with m33 & m49)		3E
ventral longitudinal muscles					
m42	IIvlm3	posterolateral process of mesofurca arm	tip of anterior metafurcal process		3E
m43	IIvlm5	lateral face of posterior mesospinal process	medial face of anterior metafurcal process		3B

Table 1. List of thoracic muscles of the cave cricket *Troglophilus neglectus*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the article. Furthermore, homologization (Hom*) according to the nomenclature after (Friedrich & Beutel 2008) is provided. *(continued)*

Present study	Hom*	Origin	Insertion	Remarks	Figure
sternocoxal muscles					
m44	IIscm1-1	lateral at mesofurcal stem	anterior mesocoxal rim (close to trochantinocoxal articulation point)		3F, 4A
m45	IIscm1-2	anterior to mesofurcal stem at mesosternum	anterior mesocoxal rim (close to m44)		3E, 4A, 4B
m46	IIscm3	ventral face of mesofurcal arm	mesal mesocoxal rim		4B
m47	IIscm4	ventral face of mesofurcal arm (posterior to m46 & m49)	lateral mesocoxal rim (close to pleurocoxal joint)		3F, 4A, 4B
m48	IIscm5	ventrolateral and dorsolateral process of mesospina	posterior mesocoxal rim		3F, 4A, 4B
m49	IIscm6	ventral face of mesofurcal arm (anterior to m46 & m47)	trochanter (with m33 & m41)		4B
m50	IIscm7	posterior face of lateral processi of mesospina	anterior metacoxal rim		3F, 4A, 4B
Metathorax					
dorsal longitudinal muscles					
m51	IIIdlm1	median region of mesophragma	median region of metaphragma	several indistinct bundles as thin musle layer	3B
dorsoventral muscles					
m52	IIIdvm2	mesophragme and anterior part of metanotum	trochantin	runs partly behind m56	3C
dorsoventral muscles					
m53	IIIdvm4	anterolateral region of metanotum	posterior metacoxal rim		3B
m54	IIIdvm5	anterolateral region of metanotum (dorsad of m53)	posterolateral metacoxal rim (close to m65)		3B
m55	IIIdvm6	osterolateral metacoxal rim (close to pleurocoxal joint)	dorsal epimeral face of metapleura (close to m57)		3C
m56	IIIdvm7	anterolateral region of metanotum (anterior to m54)	trochanter (with m63 & m68)	largest muscle in metathorax	3B
tergopleural muscles					
m57	IIItpm10	epimeral face of metapleura (dorsad of m55)	lateral region of metanotum	flattened	3C
sternopleural muscles					
m58	IIIspm2	dorsal surface of lateral metafurcal process	ventral surface of metapleural arm	strongly developed	3D
sternopleural muscles					
m59	IIIspm5	posterior face of metafurcal stem	intersegmental membrane between metathorax and abdominal pleura		3B

Table 1. List of thoracic muscles of the cave cricket *Troglophilus neglectus*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the article. Furthermore, homologization (Hom*) according to the nomenclature after (Friedrich & Beutel 2008) is provided. *(continued)*

Present study	Hom*	Origin	Insertion	Remarks	Figure
pleurocoxal muscles					
m60	IIIpcm1	anterior margin of metepisternum	trochantin		3D
m61	IIIpcm2	inner anterodorsal part of anterior margin of metepisternum (lateral to m60)	anterior metacoxal rim		3D
m62	IIIpcm3+4	dorsal metepisternum and dorsal episternal face of metapleural ridge, few fibers from metapleural arm	anterior metacoxal rim	well developed	3D
m63	IIIpcm5	dorsal part of metepisternum (dorsad of m62)	trochanter (with m56 & m68)		3C
sternocoxal muscles					
m64	IIIscm1	along lateral margin of metasternum	anterior metacoxal rim (close to trochantinocoxal joint)	broad origin	3D, 4A, 4B
m65	IIIscm2	posteroventral face of metafurcal stem	along inner posterior metacoxal rim	strongly developed, broad insertion	3C, 4A, 4B
m66	IIIscm3	ventral face of anterior and lateral metafurcal process	inner mesal metacoxal rim		3E, 4A
m67	IIIscm4	tip of posterolateral metafurcal process	lateral mesocoxal rim (close to pleurocoxal joint)	very thin and short	3C, 4A, 4B
m68	IIIscm6	distal at lateral metafurcal process	trochanter (with m56 & m63)		3F, 4B

as The nomenclature of neopteran thoracic muscles presented by Friedrich & Beutel (2008) provides a solid basis for homologizing thoracic muscles across insect groups. In some cases, however, the homologization of the thoracic muscles of *Troglophilus* with the muscles of the “generalized neopteran thorax“ (Friedrich & Beutel 2008) proves to be difficult, because muscles are solely defined by their origin and insertion points. While we were able to largely homologize the thoracic muscles unambiguously, we will discuss some problematic cases in the following:

The **M. pronoto-trochantinalis anterior** (Idvm13) and **M. pronoto-trochantinalis posterior** (Idvm14) both share the same insertion point on the trochantin and have only a slightly different origins on the pronotum: Idvm13 originates from the anterior region of the pronotum, whereas Idvm14 arises from the central region of the pronotum (Friedrich & Beutel 2008). In *Troglophilus*, the muscle m8 originates at the dorsolateral area of the

pronotum slightly above the cryptopleura, inserting at the trochantin via a long and thin tendon. As m8 is the only muscle originating from the dorsal area of the pronotum it is questionable whether m8 is homologous to Idvm13 or Idvm14. Therefore, further criteria for homologization are necessary. A similar muscle with a long thin tendon is also present in other ensiferans (Ander 1939). According to Ander (1939), the point of origin of this pronotal muscle has shifted from an anterior laterodorsal area above the cryptopleura to the lateral or central area of the pronotum behind the cryptopleura. Thus, the muscle m8 of *Troglophilus* is most likely homologous to Idvm13 according to the nomenclature of Friedrich & Beutel (2008).

The **M. profurca-phragmalis** (Idvm10) is a common feature among major polyneopteran taxa (Friedrich & Beutel 2008; Wipfler *et al.* 2015). This muscle usually connects the profurca with the prophragma. However, in some orthopteran species, like in the grasshopper *Dissosteira carolina* (59) (Snodgrass 1929) or the stick grasshopper *Cephalocoema albrechti* (59) (de Zolessi 1968), Idvm10 has an insertion point shifted to the anterior part of the mesopleura. In *Troglophilus*, both conditions are present at the same time (m7 and m12). The muscle m7 is undoubtedly homologous to Idvm10 as it arises on the dorsal face of the profurca and inserts at the ventrolateral part of the prophragma. The second muscle (m12) takes a more horizontal course and arises from the ventral surface of the profurca inserting ventrally at the anterior margin of the mesepisternum. Because of their diverging courses and their differing origins on the profurca, the muscles m7 and m12 are most likely two separate muscles and not portions of a single muscle. Therefore, we conclude that muscle m12 of *Troglophilus* is homologous to **M. profurca-intersegmentalis posterior** (Ispm5) (Friedrich & Beutel 2008). This assumption is also supported by the presence of serially homologues of m12 in the meso- and metathorax of *Troglophilus* (m36 and m59). Furthermore, a simultaneous presence of Idvm10 and Ispm5 is only known from Phasmatodea (*Megacrania tsudai*, *Carausius morosus*) and Embioptera (*Oligotoma saundersii*) (Friedrich & Beutel 2008). In contrast to the morphology of *Troglophilus*, the muscle Ispm5 is attached to the peritreme in *Megacrania* (Maki 1935) and *Oligotoma* (Maki 1938), but to the intersegmental fold in *Carausius* (Jeziorski 1918). These different attachment points cause uncertainties in regard to the homology of the muscle m12. Therefore, a question mark is added here (see Table 1).

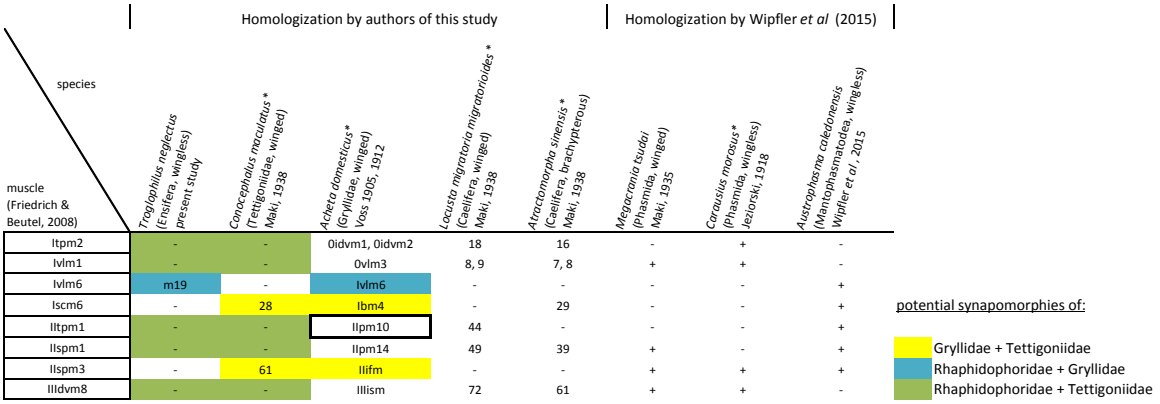
In the generalized neopteran thorax, three pterothoracic dorsoventral muscles are attached to the posterior coxal rim (Friedrich & Beutel 2008): **M. noto-coxalis anterior** (II/III dvm4), **M. noto-coxalis posterior** (II/IIIdvm5) and **M. coxa-subalaris** (II/IIIdvm6). In winged Neoptera, the muscles II/IIIdvm4 and II/IIIdvm5 originate at the central region of the nota, while II/IIIdvm6 inserts at the subalare. According to literature data (Klug 2008; Wipfler *et al.* 2015), the insertion point of II/IIIdvm6 is translocated to the lateral region of the nota in wingless Neoptera. This interpretation is consistent with the assumed tergal origin of the subalare, as proposed before (Maki 1938; Matsuda 1963, 1970). In winged orthopterans, all three dorsoventral muscles are also well developed with the muscle II/IIIdvm6 inserting at the subalare. In contrast, the same muscle inserts at the epimeral face of the pleura in wingless Orthoptera: in the cave crickets *Troglophilus neglectus* (m32 and m55; present study) and *Diestrammena asynamora* (cx-em^2) (Carpentier 1923), in the New Zealand tree weta *Hemideina femorata* (Ab4) (O'Brien & Field 2001), in the apterous proscopiids *Cephalocoema albrechti* (90a and 120) (de Zolessi 1968), in morabine grasshoppers (99 and 129) (Blackith & Blackith 1967), in wingless females of Pamphagidae, *Lamarckiana* sp. (depressor extensor muscle) (Thomas 1952), and also in micropterous species of Acrididae, e.g. *Barytettix psolus* (99 and 129) (Arbas 1983). These findings are more consistent with the assumption of a pleural origin of the subalar sclerite, as suggested by other authors (Voss 1905a; Weber 1933; Snodgrass 1935; Willkommen & Hörnschemeyer 2007; Willkommen 2009). It is noteworthy that the hypothesis of a pleural origin of the basalar and subalar plates is exclusively based on developmental studies on orthopterans. With reference to Snodgrass (1935), the aforementioned plates of nymphal Ensifera (*Gryllus*) and Caelifera (*Melanoplus*) are not yet differentiated from the pleura, and the M. coxa-subalaris (3E' and 3E'') arises from the upper edge of the pterothoracic epimeron. Voss (1905b, 1912a,b) who compared the thoracic musculature of different developmental stages of the house cricket *Acheta domesticus* also observed the epimeral insertion of the M. coxa-subalaris in the first instar (II and IIIpm6 in Voss 1905b; II and IIIldmv2 in Voss 1912a,b), in which the basalar and subalar plates (*Pleuralgelenkplatten*) are not yet present.

Muscle m37 of *T. neglectus* is not described in Orthoptera or other insect taxa (Matsuda 1970). Due to its sternal origin at the anterior face of the mesofurca and its pleural insertion at the posterior edge of the cryptopleura, this muscle should be assigned to the sterno-

pleural muscles (Friedrich & Beutel 2008). Compared with the generalized neopteran thorax, muscle m37 is likely homologous to **M. mesofurca-intersegmentalis anterior** (IIspm7) with an insertion point shifted from the intersegmental membrane/ intersegmental sclerite to the posterior edge of the propleura. A muscle connecting the intersegmental sclerite between the pro- and the mesothorax with the mesothoracic furca is present in *Corydalus* (Megaloptera) (Matsuda 1970). In Mantodea, a muscle that arises on the prosternum near the prothoracic spina inserting at the metafurca, is apparently homologous to muscle IIspm7 (Matsuda 1970; Friedrich & Beutel 2008). The specific traits of m37 in *Troglophilus* cannot be compared with the conditions reported from the aforementioned insect taxa. For this reason, we cannot homologize this muscle with any muscle listed by Friedrich & Beutel (see Table 1).

Phylogenetically informative characters

The thoracic muscles found in *Troglophilus* are compared to that of a cricket, *Acheta domesticus* (Voss 1905a,b; 1912a,b), and a bush-cricket, *Conocephalus maculatus* (Maki 1938), in order to find similarities and differences between the major ensiferan groups represented by these species. Two fully winged locusts, the African Migratory Locust *Locusta migratoria migratorioides* (Maki 1938) and European Migratory Locust *Locusta migratoria migratoria* (Albrecht 1953), and a brachypterous representative, *Atractomorpha sinensis* (Maki 1938), of the Caelifera, the sister group of Ensifera (Letsch & Simon 2013; Misof *et al.* 2014), are also considered for comparison to delineate apomorphic and plesiomorphic traits. Moreover, further taxa of Polyneoptera, either having fully developed wings or being apterous, are also studied to draw reliable conclusions about the importance and effect of winglessness on the thoracic muscular system. The phylogenetically informative characters, which have a different manifestation in the Caelifera, are compiled in figure 5. A table providing the complete data set of the thoracic muscles of the aforementioned representatives is available as an additional data file (Additional file 2).



muscle (Friedrich & Beutel, 2008) \ species	*Troglophilus neglectus* (Ensifera, wingless) present study	*Conocephalus maculatus* * (Tettigoniidae, winged) Maki, 1938	*Acheta domesticus* * (Gryllidae, winged) Voss 1905, 1912	*Locusta migratoria migratorioides* * (Caelifera, winged) Maki, 1938	*Atractomorpha sinensis* * (Caelifera, brachypterous) Maki, 1938	*Megacrania tsudai* (Phasmida, winged) Maki, 1935	*Carausius morosus* * (Phasmida, wingless) Jeziorski, 1918	*Austrophasma caledonensis* (Mantophasmatodea, wingless) Wipfler et al., 2015
	Homologization by authors of this study					Homologization by Wipfler *et al* (2015)		
ltpm2	-	-	0idvm1, 0idvm2	18	16	-	+	-
lvlm1	-	-	0vlm3	8, 9	7, 8	+	+	-
lvlm6	m19	-	lvlm6	-	-	-	-	+
lscm6	-	28	lbm4	-	29	-	-	+
lltpm1	-	-	llpm10	44	-	-	-	+
llspm1	-	-	llpm14	49	39	+	-	+
llspm3	-	61	llifm	-	-	+	+	+
llldvm8	-	-	lllism	72	61	+	+	-

potential synapomorphies of:

- Gryllidae + Tettigoniidae
- Rhaphidophoridae + Gryllidae
- Rhaphidophoridae + Tettigoniidae

Figure 5. Phylogenetically informative muscle characters of ensiferans as compared with selected members of Caelifera and other wingless/winged representatives of Polyneoptera. Common characters (= potential synapomorphic traits) are indicated by color. Direct flight muscles, as indicated by Voss (1905c, 1912b), are framed by a rectangle. Species marked with an asterisk (*) bear different names in the respective cited publication (modified after (Eades *et al.* 2015 and Brock 2014).

Discussion

Characters unique for cave crickets

Rhaphidophorids are generally considered as the most morphologically homogenous taxon within the Ensifera (Karny 1937; Ander 1939). Interestingly, rhaphidophorids are the only ensiferan subgroup for which no apomorphic character was reported in the cladistic analysis of Desutter-Grandcolas (2003). However, the thoracic muscular system of *T. neglectus* differs in significant points from that of other ensiferans, providing a number of potential autapomorphies (see Fig. 6). In general, the enlarged number of sternopleural muscles is a novelty for *Troglophilus*. In particular, the presence of m36 (IIspm6) and m37 (IIspm?) is unique within Orthoptera. *Troglophilus* is characterized by a largely reduced set of direct and indirect flight muscles. Both orthopteran representatives of the species-rich crickets (Gryllidae) and bush-crickets (Tettigoniidae) that we used for comparison are fully winged. In contrast, cave crickets completely lack wings. Thus, it is difficult to decide whether a flight muscle absent in *Troglophilus* is only a result of winglessness or represents an apomorphic character of Rhaphidophoridae. Since the ratio of flightless species to volant ones among orthopterans ranges between 30 and 60 % (Wagner & Liebherr 1992), the small taxon sampling of our study is insufficient to address this question.

	Homologization by authors of this study					Homologization by Wipfler *et al* (2015)		
species / muscle (Friedrich & Beutel, 2008)	*Troglophilus neglectus* (Ensifera, wingless) present study	*Conocephalus maculatus* * (Ensifera, winged) Maki, 1938	*Acheta domesticus* * (Ensifera, winged) Voss 1905, 1912	*Locusta migratoria migratorioides* * (Caelifera, winged) Maki, 1938	*Atractomorpha sinensis* * (Caelifera, brachypterous) Maki, 1938	*Megacrania tsudai* (Phasmida, winged) Maki, 1935	*Carausius morosus* * (Phasmida, wingless) Jeziorski, 1918	*Austrophasma caledonensis* (Mantophasmatodea, wingless) Wipfler et al , 2015
Idlm2	-	5	0dlm1	5, 6	5	+	+	+
Idvm6	-	11, 12	0ism2	15, 16	13, 14	-	-	+
Ispm1	-	14	Izm	19	(+)	-	+	+
Ispm5	+?	-	-	-	-	+	+	-
IIdlm2	-	30	IIdlm3, IIdlm4	34, 35, 36	31	+	+	+
IIdvm1	-	36	IIdvm7	40, 41, 42	34, 35, 36	-	-	-
IIdvm2	-	41	IIdvm1, IIdvm6	51	41	?	-	+
IItpm2	-	37	IIpm11	45	-	-	-	+
IItpm5	-	38	IIpm9	46	-	+	-	+
IItpm9	-	39	IIpm12, IIpm13?	47	37, 38	+	-	-
IIspm6	+	-	-	-	-	-	-	-
IIspm?	+ (IIspm7?)	-	-	-	-	-	-	-
IIItpm2	-	62	IIIpm11	74	-	-	-	+
IIItpm9	-	63	IIIpm12	76	62, 63	+	-	-
IIIspm5	+	-	-	-	-	-	-	+
IIIvlm2	-	88?	IIIvlm2-5	104?	87?	-	+	+
IIIvlm3	-	85?	IIIvlm1	103?	86?	-	-	-

Figure 6. Unique muscular characters of *Troglophilus neglectus* as compared to other polyneopteran representatives. Potential positive apomorphies are indicated in light grey. Direct flight muscles, as indicated by Voss (1905c, 1912b), are framed by a rectangle. Species marked with an asterisk (*) bear different names in the respective cited publication (modified after Eades *et al.* 2015 and Brock 2014).

It is particularly noteworthy that in *Troglophilus* the well developed musculature is important for operating the legs. These muscles are attached to the coxal rim or the trochanter and enable diverse movements of the legs. These muscles are either strongly developed, like Mm. noto-trochanteralis (m11, m33, m56), or their number is increased, like in the pro- and mesothoracic sternocoxal muscles scm1 (m23-25, m44-45). This strengthening of the sternocoxal muscles through multiplication is also reported from the wingless New Zealand tree weta *Hemideina thoracica* (O'Brien & Field 2001). M. coxo-subalaris (II/IIIdvm6), which has an additional function as a flight muscle in winged insects (Tiegs 1955), exclusively acts as leg retractor in *Troglophilus*. Additionally, *Troglophilus* has several sternopleural muscles that have not been described for other orthopterans. These include the serially homologous muscles m12 (Ispm5?), m36 (IIspm6) and m59 (IIIspm5) as well as the not homologized m37 (IIspm?). The connection of sternal and pleural elements by these muscles might lead to an enhanced movability of the thoracic segments (against each other), since there

are no rigid connections of e.g. the pterothoracic sterna as in grasshoppers (Ander 1939; Khattar & Srivastava 1962). Together with the strong leg musculature, the sternopleural musculature probably facilitates the scrambling movement of *Troglophilus* on cave walls and an increased jumping capability.

As suggested by authors of similar morphological studies (Ander 1939; Naskrecki 2000), the morphology of the thoracic sternum and associated sclerites in particular differs in decisive points between major ensiferan lineages. Including data on the thoracic skeletal anatomy of *Diestrammena asynamora* (Rhaphidophorinae) (Carpentier 1921a, 1923) and *Macropathus filifer* (Macropathinae) (Richards 1955) this specific character complex indeed provides some apomorphic traits for the Rhaphidophoridae. **Prothoracic spinasternum and prospina.** The characteristics of the prothoracic spinasternum and its internal protrusion, the prospina, have a unique appearance in rhaphidophorids. The prospinasternum of cave crickets is completely reduced externally (see Fig. 1E and Ander 1939). Its presence is only noticeable by the existence of the prospina located in the membranous fold between the pro- and the mesosternum. In other ensiferan taxa, the prospinasternum is either exposed in the sternal intersegmental fold as a fully developed sclerite or merged with the posterior part of the prosternum or the anterior part of the mesosternum (Ander 1939; Khattar & Srivastava 1962; Naskrecki 2000). Also the star-shaped prospina, consisting of paired anterolateral and posterolateral processes and an unpaired anterior process, is a unique feature of rhaphidophorids. It has also been described in *Diestrammena asynamora* (Carpentier 1921a) and *Macropathus filifer* (Richards 1955), two other representatives of cave crickets. In tettigoniids the prospina is triangular or t-shaped (Naskrecki 2000), when present. Voss (1905a) describes the prospina of *Acheta domesticus* as an irregular four-sided plate. The prospina of the mole cricket *Gryllotalpa vulgaris* is a long blade-like structure (Carpentier 1921b).

Median sclerite between meso- and metasternum. A narrow median sclerite, situated in a longitudinal arrangement between the sterna of the meso- and metathorax, is a typical feature of all rhaphidophorids (Ander 1939). This sclerite is frequently present in other ensiferan taxa, but the specific condition is different. In tettigoniids it can be rectangular or trapezoid, mostly spanning the whole width of the metasternum (Naskrecki 2000). A

triangular or semicircular sclerite is embedded at the anterior part of the metasternum in Anostostomatidae (Ander 1939; O'Brien & Field 2001), whereas in schizodactylids it is narrow and rectangular, inflexibly connecting meso- and metasternum (Khattar & Srivastava 1962; unpublished observations for *Comicus* FL). Since the anatomical situation in rhaphidophorids is similar to that found in *Grylloblatta*, Ander (1939) assumes that this sclerite is at least the posterior part of the mesothoracic spinasternum, since the mesospina is situated at the posterior end of the mesosternum right between the furcal apophyses. In contrast, Matsuda (1970) and Naskrecki (2000) refer to this sclerite as metathoracic presternum. As another alternative, Matsuda (1970) characterizes the sclerite in question as the secondarily detached anterior part of the metathoracic basisternum. Due to these uncertainties, we simply refer to the sclerite as median sclerite **ms** following Ander (1939).

Metafurca. The shape and specific structure of the metathoracic furca is another peculiarity of the thoracic skeleton of cave crickets. Rhaphidophorids possess a triramous furca with continuously tapered processes: an anterior, a lateral and a posterolateral one (see Fig. 2 and Carpentier 1921a; Richards 1955). Most other ensiferans have a biramous metafurca bearing a lateral and a posterior process (Voss 1905a; Naskrecki 2000). Like rhaphidophorids, the metafurca of Anostostomatidae has three processes, but the lateral one differs in shape from that of Rhaphidophoridae. In Anostostomatidae it is a flat, blade-like structure, termed apophysis wing, which directly projects beneath the pleural arm (O'Brien & Field 2001).

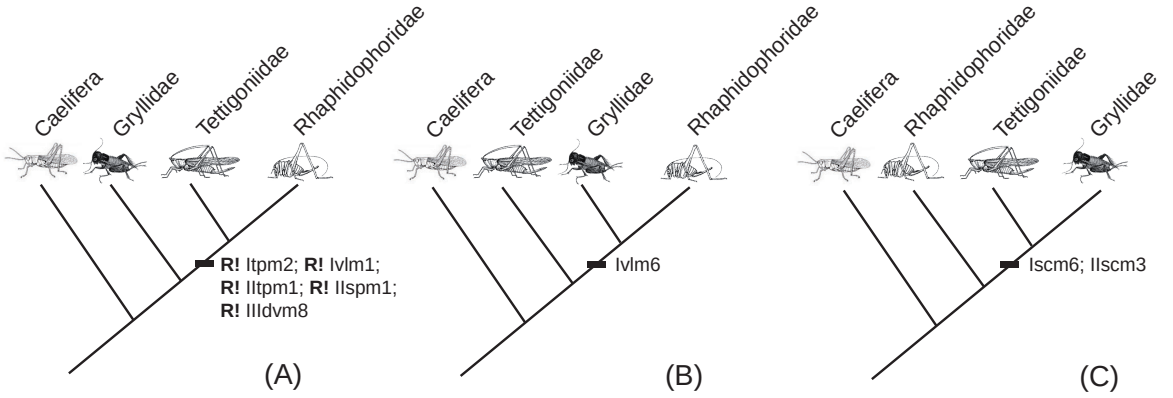


Figure 7. Informative characters of a comparative morphological study of the thoracic muscular system of representatives of Ensifera. The characters are mapped on the three competing hypotheses of the relationship between crickets (Gryllidae), bush-crickets (Tettigoniidae) and cave crickets (Rhaphidophoridae). Based on homologization in Table 1 (compiled in Additional File 2). R! indicates a reduced character in the respective taxa.

Phylogenetic implications

The scarce information available for ensiferan thorax morphology is not yet sufficient for a cladistic analysis. However, the thoracic characters found in *Troglophilus neglectus*, *Acheta domesticus* (Gryllidae) and *Conocephalus maculatus* (Tettigoniidae) in comparison to other polyneopteran representatives (see Additional file 2) shows potential synapomorphies for certain subgroups within the Ensifera. As summarized in figure 7, the most parsimonious hypothesis of the phylogenetic position of cave crickets within the Ensifera supports a closer relationship to bush-crickets (Tettigoniidae) than to true crickets (Gryllidae). Hence, the hypothesis of ensiferan relationships favoured by the majority of authors (see Additional file 1) is also supported by thoracic muscle characters. Interestingly, all of the potential synapomorphies of Rhaphidophoridae and Tettigoniidae are negative character traits, i.e. reductions. This implies that the number of thoracic muscles decreases in a specific lineage among Ensifera, viz. Rhaphidophoridae + Tettigoniiade.

On the other hand, the alternative hypotheses also gain support by few characters of the thoracic musculature (Fig. 7). Gryllidae and Rhaphidophoridae share the presence of Ivlm6. However, this ventral longitudinal muscle frequently occurs within the Polyneoptera: in *Austrophasma caledonensis* (m26) (Wipfler *et al.* 2015), *Periplaneta americana* (101) (Carbonell 1947), *Grylloblatta campodeiformis* (81) (Walker 1938), *Oligotoma saundersii* (35) (Maki 1938), and *Zorotypus hubbardi* (Ivlm6) (Friedrich & Beutel 2008). Considering the thoracic muscular system, the presence of muscle Iscm6 and IIspm3 are the unique common characters of Gryllidae and Tettigoniidae. Nevertheless, Iscm6 is also present in the outgroup representatives *Atractomorpha sinensis* (29) (Maki 1938) and *Austrophasma caledonensis* (m34) (Wipfler *et al.* 2015). Muscle Iscm6 connects the profurca with the trochanter of the foreleg. In *Troglophilus*, the profurca is relatively short and does not extend beyond the opening of the coxa. This specific morphology would not allow lscm6 to reach the trochanter, which, from a functional point of view, could explain the secondary absence in *Troglophilus*. Although lacking in the representatives of the Caelifera, muscle IIspm3 appears to represent a common character of other polyneopteran taxa since it is present e.g. in Blattodea, *Periplaneta americana* (149) (Carbonell 1947), Phasmatodea, *Carausius morosus* (IIildvm) (Jeziorski 1918) and *Megacrania tsudai* (148) (Maki 1935), Mantophasmatodea, *Austrophasma caledonensis* (m51) (Wipfler *et al.* 2015), and Zoraptera,

Zorotypus hubbardi (IIspm3) (Friedrich & Beutel 2008).

The thorax of Troglophilus neglectus *and the evolution of secondary winglessness in general*

The consequence of wing reduction and flight loss largely affects thorax morphology in insects, both cuticular structures and the muscular system, which includes secondarily undifferentiated terga, less extensive phragmata and reduced or poorly developed dorsal longitudinal muscles (II/IIIdlm1, II/IIIdlm2), as well as the absence of wing base sclerites and associated wing-steering muscles (O'Brien & Field 2001; Friedrich & Beutel 2008). These distinctive traits are also found in the thorax of *Troglophilus*. In contrast to other wingless taxa like *Grylloblatta* (Walker 1938) and the wingless morph of *Zorotypus* (Friedrich & Beutel 2008), the pleural arms in the pterothorax of *Troglophilus* are still well pronounced. Additionally, well developed pleural arms seem to be a common feature of Orthoptera, regardless the wing status, either fully winged (Voss 1905a; Snodgrass 1929), micropterous (Arbas 1983) or wingless (Carpentier 1923; de Zolessi 1968). In Mantophasmatodea, the well-developed pleural arms are explained by the climbing lifestyle among shrubs (Wipfler *et al.* 2015).

M. pleura-sternalis (II/IIIspm1), which is attached dorsally on the basalare and ventrally on the lateral part of the sternum, is thought to act as an extensor and flexor of the wing, and therefore is considered to be a direct flight muscle (Snodgrass 1929). With the exception of Grylloblattodea and Mantophasmatodea, the general trend among wingless insects is the reduction of this muscle (Wipfler *et al.* 2015). This trend is also observed within Orthoptera. In Caelifera, M. pleura-sternalis is present in the meso- and metathorax of winged locusts (Snodgrass 1929; Maki 1938), whereas it is absent in the micropterous Mexican grasshopper *Barytettix psolus* (Arbas 1983), and also reduced in wingless Proscopiidae (de Zolessi 1968) and morabine grasshoppers (Blackith & Blackith 1967). The assumption that M. pleura-sternalis is at least present in the mesothorax of Ensifera is based on the description of a single cricket species (Voss 1905b, 1912a,b). After investigation of several additional ensiferan species, we can now reliably conclude that muscle IIspm1 is only present in Grylloidea, e.g. *Acheta domesticus* (IIpm14) (Voss 1905b) and *Gryllus campestris* (ls-es[1]) (Carpentier 1923), and in the mole cricket *Gryllotalpa gryllotalpa* (LS-EP$_2$) (La Greca 1938).

The muscle is lacking in the meso- and the metathorax of the cave cricket *Troglophilus*, the schizodactylid *Comicus calcaris* (unpublished observations FL) and the winged bush-cricket *Conocephalus maculatus* (Maki 1938). This reduction of muscle spm1 in the pterothorax, especially in Tettigoniidae, might be a phylogenetically informative character, which needs to be tested in a future cladistic analysis based on an enlarged taxon sampling.

In the pterothorax of *Troglophilus*, dorsal longitudinal (II/IIIdlm2), dorsoventral (II/IIIdvm1) and tergopleural muscles (tpm) are absent, muscles that are indirectly or directly involved in flying (Friedrich & Beutel 2008; Wipfler *et al.* 2015). Most notably, the number of wing-steering tergopleural muscles is reduced, as has also been reported from other wingless taxa, e.g. Phasmatodea (Jeziorski 1918; Klug 2008) or Orthoptera (de Zolessi 1968; O'Brien & Field 2001). The only tergopleural muscle retained in both pterothoracic segments of *Troglophilus* is M. epimero-subalaris (II/IIItpm10). In winged species, this muscle connects the dorsal part of the epimeron with the subalar sclerite (Friedrich & Beutel 2008). As in *Troglophilus*, the insertion point of tpm10 is translocated to the notum in wingless species of Phasmatodea (Klug 2008) or Mantophasmatodea (Wipfler *et al.* 2015). Regarding the two major lineages of Orthoptera, Caelifera (grasshoppers) and Ensifera (katydids and crickets), muscle tpm10 is only known to exist in the meso- and metathorax of ensiferan taxa (Voss 1905b; Maki 1938; La Greca 1938). Only Maki (Maki 1938) described a muscle tpm10 in the mesothorax of the African Migratory Locust *Locusta migratoria migratorioides* (see Additional file 2), but neither Albrecht (1953) observed this muscle in the European Migratory Locust *Locusta migratoria migratoria*, nor did Snodgrass (1929) in his study about the thoracic morphology of the Carolina Grasshopper *Dissosteira carolina*. In general, the number of tergopleural muscles that have been described for *Locusta* (II/IIItpm1, II/IIItpm2, II/IIItpm5, II/IIItpm9 and IItpm10) is exceptionally large (Maki 1938). Somewhat surprisingly, only M. epimero-axillaris tertius (II/IIItpm9) is known in *Locusta migratoria migratoria* (85 and 114) (Albrecht 1953), *Dissosteira carolina* (85 and 114) (Snodgrass 1929), the wingless morabine grasshoppers (tergopleural muscle) (Blackith & Blackith 1967), and even in the brachypterous *Atractomorpha sinensis* (37/38 and 62/63) (Maki 1938). In wingless Caelifera, like *Lentula callani* (Ewer 1958) and *Cephalocoema albrechti* (de Zolessi 1968), even this muscle is reduced and not a single tergopleural muscle has ever been reported. In summary, the distinctive set of tergopleural muscles differs

significantly between Caelifera and Ensifera and the role of these muscles after wing loss is markedly dissimilar. In Euphasmatodea (the majority of extant stick insects) on the other hand, thoracic morphology of wingless species largely resembles conditions found in Ensifera. Klug (2008) observed a significantly reduced set of tergopleural muscles in wingless stick insects, only consisting of muscles II/IIItpm10 and II/IIItpm13 (tpm13 is a unique muscle of Phasmatodea). These partly comparable patterns imply that the mechanism and morphology of secondary winglessness may follow similar routes in closely related taxa. In contrast, in Embioptera (webspinners), the assumed sister taxon of Phasmatodea (Misof *et al.* 2014), the set of tergopleural muscles (II/IIItpm1, II/IIItpm5, II/IIItpm6, II/IIItpm7, II/IIItpm10; homologized in Wipfler *et al.* 2015) does not differ between winged males and wingless females of the same species (Barlet 1985a,b).

Another pattern providing support for the assumption of similar evolutionary trajectories in closely related taxa can be observed in the entirely wingless Xenonomia (Terry & Whiting 2005) comprising heelwalkers (Mantophasmatodea) and ice crawlers (Grylloblattodea). Here, the set of tergopleural muscles is different from that of wingless representatives of Orthoptera, Phasmatodea or Embioptera. *Grylloblatta campodeiformis* (Grylloblattodea) is characterized by a set of IItpm1/5 and IIItpm1/5 (Walker 1938) (homologized in Friedrich & Beutel 2008). Based on the description of Klug (Klug 2008), *Austrophasma caledonensis* (Mantophasmatodea) exhibits the same set of tergopleural muscles in the pterothorax, IItpm1/5 and IIItpm1/5. According to the reinvestigation of the same species (Wipfler *et al.* 2015) a considerably higher number of tergopleural muscles is reported: IItpm1/2/3/4/5/?10 and IIItpm1/2/3/4/5/?10. Both studies are based on µCT-data sets, albeit different ones. Depending on the quality of the data sets, it is possible that some muscles were initially overlooked, e.g. tpm10 characterized as a flat muscle closely fitting the skeletal elements. Nevertheless, muscle tpm1 in Klug (2008) and the four muscles tpm1/2/3/4 described for *Austrophasma* by Wipfler *et al.* (2015) are located in the same small area between the anterior part of the tergum and the dorsal part of the pleural ridge. A further explanation of these striking differences might lie in the different life stages or sexes investigated in both studies. Klug (2008) examined a nymphal stage of unknown sex of *Austrophasma caledonensis*, whereas in the study of Wipfler *et al.* (2015) no explicit information about the developmental stage or the sex of the investigated specimens is provided. However, studies

about the postembryonic development of the flight musculature of hemimetabolous insects show that these muscles are less developed in early nymphal stages, significantly increasing in size during their ontogenesis (Wiesend 1957; Ready & Josephson 1982; Ready & Najm 1985; Marden 2000). Other studies comparing the thoracic musculature report a differing number of muscles in nymphs and adults of the same species (Voss 1905b, 1912a; Büsse *et al.* 2015). In consequence, the presence of tpm1 and tpm5 in the meso- and metathorax of Grylloblattodea and Mantophasmatodea might still be considered a synapomorphic character of both taxa.

Principally, the flight ability and performance of insects also depend on the total mass of flight muscles present, and not only on the concrete set of direct and indirect flight muscles (Marden 2000). Nonetheless, the concrete set of tergopleural muscles differs between major insect groups (Friedrich & Beutel 2008). Regarding the Orthoptera, their flight ability and performance become of secondary importance, since many species primarily move by jumping. In these cases, wings are mainly used to control the direction and trajectory during the jumping process (Voss 1905c; Beier 1972). For instance, the house cricket *Acheta domesticus* (Voss 1905b), with a set of IItpm1/2/5/9/10 and IIItpm1/2/5/9/10, and the tettigoniid *Conocephalus (Anisoptera) maculatus* (Maki 1938), with a reduced set of IItpm2/5/9 and IIItpm2/9/10, exhibit similar flight capability (Voss 1905c; Maki 1938). On the other hand, the absence of specific tergopleural muscles as in the brachypterous gaudy grasshopper *Atractomorpha sinensis* (Maki 1938) having only a single duplicated tergopleural muscle in the meso- and metathorax (II/IIItpm9) causes a low vagility (John & King 1983). In contrast, *Sipyloidea sipylus*, a winged stick insect, only has the ability to control its speed and trajectory during free fall with a set of six different metathoracic tergopleural muscles in the flight apparatus (tpm1/3/4/6/9/10) (Maginnis 2006; Klug 2008). In conclusion, there appears to be no correlation between an increased number of pterothoracic tergopleural muscles and an enhanced flight capability. However, an extremely reduced set of tergopleural muscles does consequently lead to the inability to fly.

Anatomical structures that are no longer used will be reduced in the course of evolution, and the degree of reduction can be an indicator of the time elapsed (Mahner & Bunge 1997). Nevertheless, conservative anatomical elements can be retained although asso-

ciated traits of the periphery are lost (Kutsch & Kittmann 1991). As we have outlined, the loss of wings in insect groups like Orthoptera, Xenonomia (Wipfler *et al.* 2015) or Phasmatodea (Klug 2008) has been followed by a number of anatomical adaptations of skeletal and muscular elements in the thorax. The insect lineages compared above exhibit significantly different evolutionary histories in regard of the time span since wing loss, affecting the degree of reduction or anatomical adaptations towards flightlessness. The radiation of Rhaphidophoridae began at least 140 million years ago (Allegrucci *et al.* 2010; Song *et al.* 2015). Thus, the Rhaphidophoridae may represent the oldest exclusively wingless lineage within Ensifera (Song *et al.* 2015), and wing loss occurred most probably in the last common ancestor (autapomorphy) of all Rhaphidophoridae. The likewise wingless Xenonomia, heelwalkers (Mantophasmatodea) + ice crawlers (Grylloblattodea), are roughly the same age as the Rhaphidophoridae (Misof *et al.* 2014). We have demonstrated that the thoracic musculature differs significantly in both lineages. In comparison, the wingless representatives of Euphasmatodea are significantly younger. The diversification of their major extant lineages took place during a period of about 20 million years, and presumably started after the Cretaceous-Tertiary boundary ~66 million years ago (Bradler & Buckley 2011; Bradler *et al.* 2015). The thoracic musculature of wingless Ensifera, Rhaphidophoridae in particular, is most similar to the conditions found in the much younger wingless representatives of Euphasmatodea than in the equally old Xenonomia, refuting any dependency between level of reduction and evolutionary time. This might be explained by the degree of correlation of the structures in question to other, still adaptive features (Mahner & Bunge 1997).

Conclusions

Secondary winglessness, a widespread phenomenon among pterygote insects, largely affects the thoracic anatomy including skeletal structures and the muscular system. By comparing the thoracic morphology of various wingless representatives of Polyneoptera, we demonstrate that anatomical adaptations towards flightlessness, especially regarding the flight musculature, are highly homogenous within major lineages, viz. Ensifera, Caelifera, Xenonomia, or Euphasmatodea. However, in most cases these specific adaptations are strikingly different between the aforementioned taxa indicating a markedly dissimilar role of these muscles after wing loss.

The thoracic morphology of Ensifera is a highly structured character complex whose investigation is a worthwhile endeavor, leading to a deeper understanding of functional adaptations during the evolution of Ensifera in general. We have shown that the thoracic morphology can be a valuable source for characterizing individual ensiferan taxa, providing a number of potential apomorphies for cave crickets (Rhaphidophoridae). Based on our comparison with other ensiferans, we can provide arguments for a closer relationship of Rhaphidophoridae to Tettigoniidae, rather than to Gryllidae. These findings are consistent with previous assumptions (Gwynne 1995; Desutter-Grandcolas 2003; Song *et al.* 2015).

References

Albrecht, F. O. 1953. *The Anatomy of the Migratory Locust*. University of London, Athlone Press, Western Printing Services Ltd., London, 1-118 pp.

Allegrucci, G., Trewick, S. A., Fortunato, A., Carchini, G. & Sbordoni, V. 2010. Cave crickets and cave weta (Orthoptera, Rhaphidophoridae) from the southern end of the World : a molecular phylogeny test of biogeographical hypotheses. *Journal of Orthoptera Research*, **19**, 121–130.

Ander, K. 1939. Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria). *Opuscula Entomologica Supplementum II*, 1–306.

Arbas, E. A. 1983. Thoracic morphology of a flightless mexican grasshopper, *Barytettix psolus*: comparison with the locust, *Schistocerca gregaria*. *Journal of Morphology*, **176**, 141–153.

Barlet, J. 1985a. La musculature pterothoracique d'une *Embia* femelle (Insectes, Embiopteres). *Bulletin de la Société Royale des Sciences de Liège*, **54**, 140–148.

Barlet, J. 1985b. Le pterothorax du male d'*Embia surcoufi* Navas (Insectes, Embiopteres). *Bulletin de la Société Royale des Sciences de Liège*, **54**, 349–362.

Beier, M. 1972. Saltatoria (Grillen und Heuschrecken). *In*: Helmcke, J. G., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–217.

Blackith, R. E. & Blackith, R. M. 1967. The anatomy and physiology of the morabine grasshoppers. III. muscles, nerves, tracheae, and genitalia. *Australian Journal of Zoology*, **15**, 961–998.

Bradler, S. & Buckley, T. R. 2011. Stick insect on unsafe ground: does a fossil from the early Eocene of France really link Mesozoic taxa with the extant crown group of Phasmatodea? *Systematic Entomology*, **36**, 218–222.

Bradler, S., Cliquennois, N. & Buckley, T. R. 2015. Single origin of the Mascarene stick insects: ancient radiation on sunken islands? *BMC Evolutionary Biology*, **15**, 196.

Brock, P. D. 2014. Phasmida Species File. Version 5.0/5.0. http://phasmida.speciesfile.org. Accessed 5 Jul 2015.

Büsse, S. & Hörnschemeyer, T. 2013. The thorax musculature of Anisoptera (Insecta: Odonata) nymphs and its evolutionary relevance. *BMC Evolutionary Biology*, **13**, 237.

Büsse, S., Helmker, B. & Hörnschemeyer, T. 2015. The thorax morphology of *Epiophlebia* (Insecta: Odonata) nymphs – including remarks on ontogenesis and evolution. *Scientific Reports*, **5**, 12835.

Carbonell, C. S. 1947. The thoracic muscles of the cockroach *Periplaneta americana* (L.). *Smithsonian Miscellaneous Collections*, **107**, 1–23.

Carpentier, F. 1921a. Pterothorax et prothorax. Etude des segments thoraciques d'un orthoptère. *Annales de la Société Entomologique de Belgique*, **61**, 337–343.

Carpentier, F. 1921b. Sur l'endosquelette prothoracique de *Gryllotalpa vulgaris*. *Bulletin de la Classe des Sciences, Académie Royale de Belgique*, **7**, 125–134.

Carpentier, F. 1923. Musculature et squelette chitineux: Recherches sur le comportement de la musculature des flancs dans les segments cryptopleuriens du thorax chez les orthoptères. *Mémoires de l' Académie Royale de Belgique (2). Collection in -8°*, **7 (3)**, 1–56.

de Zolessi, L. C. 1968. Morphologie, endosquelette et musculature d'un acridien aptère (Orthoptera: Proscopiidae). *Transactions of the Royal Entomological Society of London*, **120**, 55–113.

Desutter-Grandcolas, L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta*, **32**, 525–561.

Eades, D. C., Otte, D., Cigliano, M. M. & Braun, H. 2015. Orthoptera Species File. Version 5.0/5.0. http://orthoptera.speciesfile.org. Accessed 28 Mar 2015.

Edmunds, M. 1974. *Defence in Animals: A Survey of Anti-Predator Defences*. Longman, New York, 357 pp.

Ewer, D. W. 1958. Notes on acridid anatomy. V. The pterothoracic musculature of *Lentula callani* Dirsh. *Journal of the Entomological Society of Southern Africa*, **21**, 132–138.

Fenn, J. D., Song, H., Cameron, S. L. & Whiting, M. F. 2008. A preliminary mitochondrial genome phylogeny of Orthoptera (Insecta) and approaches to maximizing phylogenetic signal found within mitochondrial genome data. *Molecular Phylogenetics and Evolution*, **49**, 59–68.

Field, L. H. 1993. Structure and evolution of stridulatory mechanisms in New Zealand wetas (Orthoptera: Stenopelmatidae). *International Journal of Insect Morphology and Embryology*, **22**, 163–183.

Flook, P. K., Klee, S. & Rowell, C. H. 1999. Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. *Systematic Biology*, **48**, 233–253.

Friedrich, F. & Beutel, R. G. 2008. The thorax of *Zorotypus* (Hexapoda, Zoraptera) and a new nomenclature for the musculature of Neoptera. *Arthropod Structure & Development*, **37**, 29–54.

Friedrich, F., Farrell, B. D. & Beutel, R. G. 2009. The thoracic morphology of Archostemata and the relationships of the extant suborders of Coleoptera (Hexapoda). *Cladistics*, **25**, 1–37.

Friedrich, F., Matsumura, Y., Pohl, H., Bai, M., Hörnschemeyer, T. & Beutel, R. G. 2013. Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. *Entomological Science*, **17**, 1–24.

Giribet, G. 2015. Morphology should not be forgotten in the era of genomics—a phylogenetic perspective. *Zoologischer Anzeiger - A Journal of Comparative Zoology*, **256**, 96–103.

Gorochov, A. V. 1995. System and evolution of the suborder Ensifera (Orthoptera). *Proceedings of the Zoological Institute, Russian Academy of Sciences*, 1–224 (in Russian).

Gwynne, D. T. 1995. Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research*, **4**, 203–218.

Handlirsch, A. 1929. Saltatoria oder Heuschrecken. *In*: Kükenthal, W. & Krumbach, T. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 692–750.

Hubbell, T. H. & Norton, R. M. 1978. The systematics and biology of the cave-crickets of the North American tribe Hadenoecini (Orthoptera Saltatoria: Ensifera: Rhaphidophoridae: Dolichopodinae). *Miscellaneous Publications Museum of Zoology, University of Michigan*, **156**, 1–124.

Jeziorski, L. 1918. Der Thorax von *Dixippus morosus* (*Carausius*). *Zeitschrift für Wissenschaftliche Zoologie*, **117**, 727–815.

John, B. & King, M. 1983. Population cytogenetics of *Atractomorpha similis*. *Chromosoma*, **88**, 57–68.

Jost, M. C. & Shaw, K. L. 2006. Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution*, **38**, 510–530.

Karny, H. H. 1921. *Zur Systematik der orthopteroiden Insekten*. G. Koleff & Company, Weltevreden, 269 pp.

Karny, H. H. 1934. Zur Kenntnis der ostasiatischen Rhaphidophorinen (Orth. Salt. Gryllacrididae). *Konowia*, **13**, 70–80.

Karny, H. H. 1937. Orthoptera. Fam. Gryllacrididae. *Genera Insectorum*, **206**, 1–317.

Khattar, N. & Srivastava, R. P. 1962. Morphology of the pterothorax of *Schizodactylus monstrosus* Don. (Orthoptera). *Journal of the Zoological Society of India*, **14**, 93–108.

Kingsolver, J. G. 1985. Butterfly thermoregulation: organismic mechanisms and population consequences. *Journal of Research on the Lepidoptera*, **24**, 1–20.

Klug, R. 2008. *Anatomie des Pterothorax der Phasmatodea, Mantophasmatodea und Embioptera und seine Bedeutung für die Phylogenie der Polyneoptera (Insecta).* Georg-August-Universität Göttingen, 1-126 pp.

Koeth, M., Friedrich, F., Pohl, H. & Beutel, R. G. 2012. The thoracic skeleto-muscular system of *Mengenilla* (Strepsiptera: Mengenillidae) and its phylogenetic implications. *Arthropod Structure & Development*, **41**, 323–335.

Kutsch, W. & Kittmann, R. 1991. Flight motor pattern in flying and non-flying Phasmida. *Journal of Comparative Physiology A*, **168**, 483–490.

La Greca, M. 1938. La muscolatura di *Gryllotalpa gryllotalpa* (L.). *Archivio Zoologico Italiano*, **27**, 217–319.

Legendre, F., Robillard, T., Song, H., Whiting, M. F. & Desutter-Grandcolas, L. 2010. One hundred years of instability in ensiferan relationships. *Systematic Entomology*, **35**, 475–488.

Letsch, H. & Simon, S. 2013. Insect phylogenomics: new insights on the relationships of lower neopteran orders (Polyneoptera). *Systematic Entomology*, **38**, 783–793.

Maginnis, T. L. 2006. Leg regeneration stunts wing growth and hinders flight performance in a stick insect (*Sipyloidea sipylus*). *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1811–1814.

Mahner, M. & Bunge, M. 1997. *Foundations on Biophilosophy*. Springer-Verlag, Berlin, 423 pp.

Maki, T. 1935. A study of the musculature of the phasmid *Megacrania tsudai* Shiraki. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University*, **12**, 1–279.

Maki, T. 1938. Studies on the thoracic musculature of insects. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University*, **24**, 1–343.

Marden, J. H. 2000. Variability in the size, composition, and function of insect flight muscles. *Annual Reviews of Physiology*, **62**, 157–178.

Matsuda, R. 1963. Some evolutionary aspects of the insect thorax. *Annual Review of Entomology*, **8**, 59–76.

Matsuda, R. 1970. Morphology and evolution of the insect thorax. *Memoirs of the Entomological Society of Canada*, **76**, 1–431.

Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, a., Mayer, C., Frandsen, P. B., Ware, J., Flouri, T., Beutel, R. G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, a. J., Aspock, U., Aspock, H., Bartel, D., Blanke, a., Berger, S., Bohm, a., Buckley, T. R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L. S., Kawahara, a. Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D. D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J. L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B. M., Schutte, K., Sekiya, K., Shimizu, S., Slipinski, a., Stamatakis, a., Song, W., Su, X., Szucsich, N. U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M. G., Wiegmann, B. M., Wilbrandt, J., Wipfler, B., Wong, T. K. F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D. K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Xu, X., Yang, H., Wang, J., Kjer, K. M. & Zhou, X. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.

Naskrecki, P. 2000. *The Phylogeny of Katydids (Insecta: Orthoptera: Tettigoniidae) and the Evolution of Their Acoustic Behaviour.* University of Conneticut, 403 pp.

O'Brien, B. & Field, L. H. 2001. Morphology and anatomy of New Zealand wetas. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New York, 127–162.

Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research*, **1**, 25–49.

Ready, N. E. & Josephson, R. K. 1982. Flight muscle development in a hemimetabolous insect. *Journal of Experimental Zoology*, **220**, 49–56.

Ready, N. E. & Najm, R. E. 1985. Structural and functional development of cricket wing muscles. *Journal of Experimental Zoology*, **233**, 35–50.

Rentz, D. C. 2010. *A Guide to the Katydids of Australia*. CSIRO Publishing, Collingwood, 1-214 pp.

Richards, A. M. 1955. The anatomy and morphology of the cave-orthopteran *Macropathus filifer* Walker, 1869. *Transactions of the Royal Society of New Zealand*, **83**, 405–452.

Robinson, D. J. & Hall, M. J. 2002. Sound signalling in Orthoptera. *In*: Evans, P. (ed.) *Advances in Insect Physiology*. Elsevier Ltd, 151–278.

Rowell, C. H. F. & Flook, P. K. 1998. Phylogeny of the Caelifera and the Orthoptera as derived from ribosomal gene sequences. *Journal of Orthoptera Research*, **7**, 147–156.

Sharov, A. G. 1968. Phylogeny of the Orthopteroidea. *Transactions of the Institute of Paleontology. Academy of Sciences of the USSR.*, **118**, 1–251.

Sheffield, N. C., Hiatt, K. D., Valentine, M. C., Song, H. & Whiting, M. F. 2010. Mitochondrial genomics in Orthoptera using MOSAS. *Mitochondrial DNA*, **21**, 87–104.

Snodgrass, R. E. 1929. The thoracic mechanism of a grasshopper, and its antecedents. *Smithsonian Miscellaneous Collections*, **82**, 1–111.

Snodgrass, R. E. 1935. *Principles of Insect Morphology*. 1993rd ed. McGraw-Hill, Inc., New York, London, 1-667 pp.

Song, H., Am, C., Marta, M., Desutter-, L., Heads, S. W., Huang, Y., Otte, D. & Whiting, M. F. 2015. 300 million years of diversification : elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics*, **31**, 621–651.

Strauß, J. & Lakes-Harlan, R. 2008. Neuroanatomy of the complex tibial organ of *Stenopelmatus* (Orthoptera: Ensifera: Stenopelmatidae). *The Journal of Comparative Neurology*, **511**, 81–91.

Strauß, J. & Lakes-Harlan, R. 2009. The evolutionary origin of auditory receptors in Tettigonioidea: the complex tibial organ of Schizodactylidae. *Naturwissenschaften*, **96**, 143–146.

Strauß, J. & Stumpner, A. 2015. Selective forces on origin, adaptation and reduction of tympanal ears in insects. *Journal of Comparative Physiology A*, **201**, 155–169.

Stritih, N. & Čokl, A. 2012. Mating behaviour and vibratory signalling in non-hearing cave crickets reflect primitive communication of Ensifera. *PloS ONE*, **7**, e47646.

Stumpner, A., Stritih, N., Mai, O. & Bradler, S. 2015. Diversity of Orthoptera in the south-western Karst-region of Slovenia with notes on acoustics and species identification. *Acta Entomologica Slovenica*, **23**, 5–20.

Terry, M. D. & Whiting, M. F. 2005. Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics*, **21**, 240–257.

Thomas, J. G. 1952. A comparison of the pterothoracic skeleton and flight muscles of male and female *Lamarckiana* species (Orthoptera, Acrididae). *Proceedings of the Zoological Society of London*, **27**, 1–12.

Tiegs, O. W. 1955. The flight muscles of insects - their anatomy and histology; with some observations on the structure of striated muscle in general. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **238**, 221–359.

Voss, F. 1905a. Über den Thorax von *Gryllus domesticus*. Erster Teil. Das Skelett. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (2)**, 268–514.

Voss, F. 1905b. Über den Thorax von *Gryllus domesticus*. Zweiter Teil. Die Muskulatur. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 355–521.

Voss, F. 1905c. Über den Thorax von *Gryllus domesticus*. Dritter Teil. Die Mechanik. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 645–696.

Voss, F. 1912a. Über den Thorax von *Gryllus domesticus*. Fünfter Teil. Die nachembryonale Metamorphose im ersten Stadium. *Zeitschrift für Wissenschaftliche Zoologie*, **100**, 589–834.

Voss, F. 1912b. Über den Thorax von *Gryllus domesticus*. Fünfter Teil. Die nachembryonale Metamorphose im ersten Stadium. Erste Fortsetzung. *Zeitschrift für Wissenschaftliche Zoologie*, **101**, 445–578.

Wagner, D. L. & Liebherr, J. K. 1992. Flightlessness in insects. *Trends in Ecology & Evolution*, **7**, 216–220.

Walker, E. M. 1938. On the anatomy of *Gylloblatta campodeiformis* Walker. 3. Exoskeleton and musculature of the neck and thorax. *Annals of the Entomological Society of America*, **31**, 588–640.

Weber, H. 1933. *Lehrbuch Der Entomologie*. Gustav Fischer Verlag, Jena, 726 pp.

Wiesend, P. 1957. Die postembryonale Entwicklung der Thoraxmuskulatur bei einigen Feldheuschrecken mit besonderer Berücksichtigung der Flugmuskeln. *Zeitschrift für Morphologie und Ökologie der Tiere*, **46**, 529–570.

Willkommen, J. 2009. The tergal and pleural wing base sclerites – homologous within the basal branches of Pterygota? *Aquatic Insects*, **31**, 443–457.

Willkommen, J. & Hörnschemeyer, T. 2007. The homology of wing base sclerites and flight muscles in Ephemeroptera and Neoptera and the morphology of the pterothorax of *Habroleptoides confusa* (Insecta: Ephemeroptera: Leptophlebiidae). *Arthropod Structure & Development*, **36**, 253–269.

Wipfler, B., Klug, R., Ge, S.-Q., Bai, M., Göbbels, J., Yang, X.-K. & Hörnschemeyer, T. 2015. The thorax of Mantophasmatodea, the morphology of flightlessness, and the evolution of the neopteran insects. *Cladistics*, **31**, 50–70.

Zeuner, F. E. 1939. *Fossil Orthoptera Ensifera*. British Museum (Natural History), London, 1-321 pp.

Zhang, H.-L., Huang, Y., Lin, L.-L., Wang, X.-Y. & Zheng, Z.-M. 2013. The phylogeny of the Orthoptera (Insecta) as deduced from mitogenomic gene sequences. *Zoological Studies*, **52**, 37.

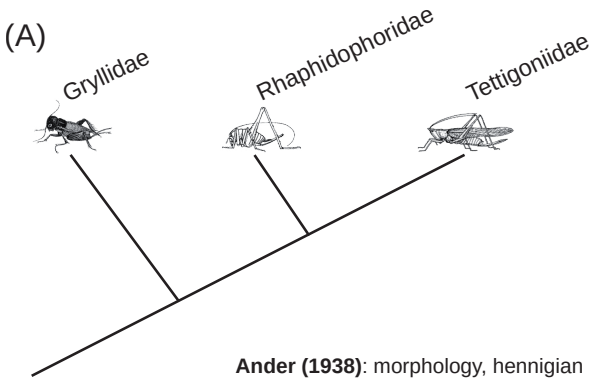
Zhou, Z., Shi, F. & Zhao, L. 2014. The first mitochondrial genome for the superfamily Hagloidea and implications for its systematic status in Ensifera. *PloS ONE*, **9**, e86027.

Acknowledgements

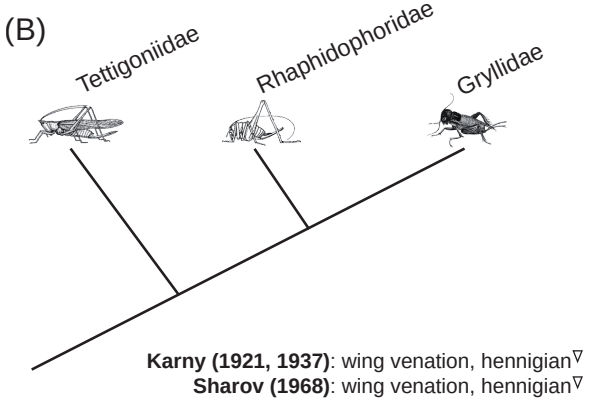
We thank Dr. Christian Fischer, University of Göttingen, for providing useful critiques and helpful comments on the manuscript. The project was funded through the DFG grant HO2306/10-1 and publication was supported by the Open Access Publication Funds of the University of Göttingen.

Authors' contributions

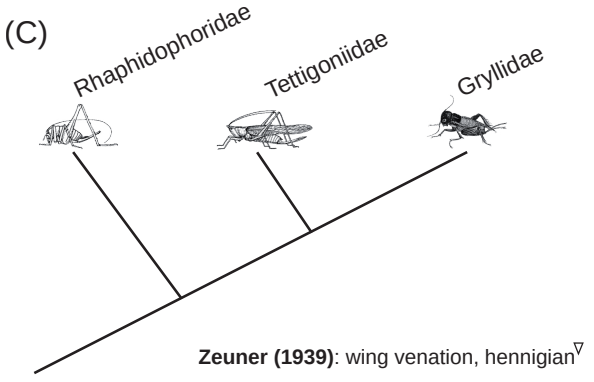
SB collected and fixed the material. TH performed the SRμCT-scan. FL generated data, conducted photographical documentation, performed the three-dimensional reconstruction, and wrote the initial draft. SB and TH designed the study. SB supervised research, contributed to writing the manuscript and data discussion. TH commented on the manuscript and contributed to data discussion. All authors approved the final version of the manuscript.



Ander (1938): morphology, hennigian
Gwynne (1995): morphology*
Gorochov (1995): morphology (incl. wings), hennigian∇
Flook et al (1999): mitochondrial + nuclear rDNA*
Desutter-Grandcolas (2003): morphology*
Fenn et al (2008): mitochondrial genome*
Sheffield et al (2010): mitochondrial genome*
Zhang et al (2013): cytochrome oxidase + cytochrome b*
Zhou et al (2014): mitochondrial genome*
Song et al (2015): mitochondrial genome + nuclear genes*



Karny (1921, 1937): wing venation, hennigian∇
Sharov (1968): wing venation, hennigian∇
Jost & Shaw (2006): 18S, 28S, 16SrDNA*



Zeuner (1939): wing venation, hennigian∇

Additional File 1. Competing hypotheses of the relationships between true crickets (Gryllidae), bush-crickets (Tettigoniidae) and cave crickets (Rhaphidophoridae) following different authors. Further ensiferan taxa are excluded in this scheme. Studies marked by an asterisk (*) are based on formally cladistic analyses, studies tagged with a triangle include fossils.

Additional File 2. Thoracic muscles of different representatives of Polyneoptera homologized following nomenclature by (Friedrich & Beutel 2008).

		Homologization by author					Homologization by Wipfler *et al* (2015)		
	species / muscle (Friedrich & Beutel, 2008)	*Troglophilus neglectus* (Rhaphidophoridae) (present study)	*Conocephalus maculatus* * (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* * (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* * (Caelifera, winged) (Maki, 1938)	*Atractomorpha sinensis* * (Caelifera, macropterous) (Maki, 1938)	*Megacrania tsudai* (Phasmida, winged) (Maki, 1935)	*Carausius morosus** (Phasmida wingless) (Jeziorski, 1918)	*Austrophasma caledonensis* (Mantophasmatodea wingless) Wipfler *et al* (2015)
PROTHORAX	Idlm1	+	1	0dlm2	1	1	?	?	+
	Idlm2	-	5	0dlm1	5, 6	5	+	+	+
	Idlm3	+	2	odlm1a	2	2	-	-	+
	Idlm4	-	4	-	-	-	-	+	+
	Idlm5	+	3	Idlm3a, Idlm3b	3 (2 bundles), 4	3, 4	+	+	+
	Idlm6	-	-	-	-		-	-	-
	Idvm1	+	7	0dvmδ	11	10	-	-	-
	Idvm2	+	9	0dvmγ	13	11	+	+	+
	Idvm3	+	10	0dvmβ	14	12	+	+	+
	Idvm4	-	-	0dvmα, Odvmα'	-	-	+	+	+
	Idvm5	+	-	0ism	-	-	-	+	+
	Idvm6	-	11, 12	0ism2	15, 16	13, 14	-	-	+
	Idvm7	-	-	-	-	-	-	-	-
	Idvm8	-	-	-	-	-	-	-	-
	Idvm9	-	-	-	-	-	-	-	-
	Idvm10	+	13	Iism	17	15	+	+	+
	Idvm11	-	-	-	-	-	+	+	-
	Idvm12	-	-	-	-	-	-	-	-
	Idvm13	+	15	Idvm1 (1905) Idvm6 (1912)	20	17	+	+	+
	Idvm14	-	-	-	-		?	+	+
	Idvm15	-	-	-	-	-	+	+	+
	Idvm16	+	18	Idvm2	22	20	+	+	+
	Idvm17	+ ?	19	Idvm7	23	21	+	+	+
	Idvm18	- ?	20	Ipm6	24	22	+	+	+
	Idvm19	+	25	Idvm8, Ipm6a	30	27	-	+	+
	Itpm1	-	-	0vlm5a	-	-	-	-	-
	Itpm2	-	-	0idvm1, 0idvm2	18	16	-	+	-

Additional File 2. Thoracic muscles of different representatives of Polyneoptera homologized following nomenclature by (Friedrich & Beutel 2008). *(continued)*

	Homologization by author					Homologization by Wipfler *et al* (2015)		
species / muscle (Friedrich & Beutel, 2008)	*Troglophilus neglectus* (Rhaphidophoridae) (present study)	*Conocephalus maculatus* * (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* * (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* * (Caelifera, winged) (Maki, 1938)	*Atractomorpha sinensis* * (Caelifera, macropterous) (Maki, 1938)	*Megacrania tsudai* (Phasmida, winged) (Maki, 1935)	*Carausius morosus* * (Phasmida wingless) (Jeziorski, 1918)	*Austrophasma caledonensis* (Mantophasmatodea wingless) Wipfler *et al* (2015)
ltpm3	-	-	-	-	-	+	-	+
ltpm4	-	-	lpm9, lpm11, lpm12	-	-	+	-	+
ltpm5	-	-	- ?	-	-	-	-	-
ltpm6	-	-	-	-	-	-	-	?
lspm1	-	14	lzm	19	(+)*	-	+	+
lspm2	-	-	-	-	-	+	+	+
lspm3	-	34	-	-	-	-	-	?
lspm4	-	-	-	-	-	-	-	-
lspm5	+	-	-	-	-	+	+	-
lspm6	-	-	-	-	-	-	-	-
lspm7	-	-	-	-	-	-	-	-
lpcm1	-	-	-	-	-	-	-	-
lpcm2	+	16	0vlm2	-	-	-	-	-
lpcm3	-	-	lpm5	-	18	+	-	-
lpcm4	+	23	lpm4	28	26	+	+	+
lpcm5	+	24	?	29	25	-	-	-
lpcm6	-	-	-	-	-	+	+	-
lpcm7	-	-	-	-	-	-	-	-
lpcm8	+ (2 bundles)	26, 27	lpm4a, ldvm5	31, 32	28	+	+	+
lvlm1	-	-	0vlm3	8, 9	7, 8	+	+	-
lvlm2	-	-	-	-		-	-	-
lvlm3	+	6	0vlm4, 0vlm5	7	6	+	+	+
lvlm4	+	8	lvlm7	12	-	+	+	+
lvlm5	-	-	-	-	-	-	-	-
lvlm6	+	-	lvlm6	-	-	-	-	+
lvlm7	+	31	lvlm4, lvlm5	37	32	-	-	+
lvlm8	+ (paired)	32 (unpaired)	lvlm1 (unpaired)	38 (unpaired)	-	-	-	-
lvlm9	+	33	lvlm3	39	33	-	-	-

Additional File 2. Thoracic muscles of different representatives of Polyneoptera homologized following nomenclature by (Friedrich & Beutel 2008). *(continued)*

		Homologization by author					Homologization by Wipfler *et al* (2015)		
	species / muscle (Friedrich & Beutel, 2008)	*Troglophilus neglectus* (Rhaphidophoridae) (present study)	*Conocephalus maculatus* * (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* * (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* * (Caelifera, winged) (Maki, 1938)	*Atractomorpha sinensis* * (Caelifera, macropterous) (Maki, 1938)	*Megacrania tsudai* (Phasmida, winged) (Maki, 1935)	*Carausius morosus* * (Phasmida wingless) (Jeziorski, 1918)	*Austrophasma caledonensis* (Mantophasmatodea wingless) Wipfler *et al* (2015)
	Iscm1	+ (3x)	17	Ibm1	21	19	+	+	+
	Iscm2	+	21	Ibm2	-	-	+	+	+
	Iscm3	+	22	Ibm3	27	24	+	+	+
	Iscm4	-	-	-	-	-	-	-	+
	Iscm5	+	-	Ibm7	25, 26	23	-	-	-
	Iscm6	-	28	Ibm4	-	29	-	-	+
	Iscm7	+	43	Ivlm2	-	-	-	-	-
MESOTHORAX	IIdlm1	+	29	IIdlm1, IIdlm2	33	30	-	-	+
	IIdlm2	-	30	IIdlm3, IIdlm4	34, 35, 36	31	+	+	+
	IIdvm1	-	36	IIdvm7	40, 41, 42	34, 35, 36	-	-	-
	IIdvm2	-	41	IIdvm1, IIdvm6	51	41	?	-	+
	IIdvm3	-	-	-	58?	-	+	+	+
	IIdvm4	+	45	IIdvm3+4	53	43	+	+	+
	IIdvm5	+	46	IIdvm2	54	44	+	+	+
	IIdvm6	+	47	IIpm6	55	45	+	+	+
	IIdvm7	+	54	IIdvm5	62	52, 53	+	+	+
	IIdvm8	-	-	Iiism	43	-	+	+	-
	IIdvm9	-	-	-	-	-	+	+	-
	IItpm1	-	-	IIpm10	44	-	-	-	+
	IItpm2	-	37	IIpm11	45	-	-	-	+
	IItpm3	-	-	-	-	-	-	-	+
	IItpm4	-	-	-	-	-	-	-	+
	IItpm5	-	38	IIpm9	46	-	+	-	+
	IItpm6	-	-	-	-	-	+	-	-
	IItpm7	-	-	-	-	-	-	-	-
	IItpm8	-	-	IIpm13?	-	-	-	-	-
	IItpm9	-	39	IIpm12, IIpm13?	47	37, 38	+	-	-

Additional File 2. Thoracic muscles of different representatives of Polyneoptera homologized following nomenclature by (Friedrich & Beutel 2008). *(continued)*

	Homologization by author					Homologization by Wipfler *et al* (2015)		
species / muscle (Friedrich & Beutel, 2008)	*Troglophilus neglectus* (Rhaphidophoridae) (present study)	*Conocephalus maculatus* * (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus** (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* * (Caelifera, winged) (Maki, 1938)	*Atractomorpha sinensis* * (Caelifera, macropterous) (Maki, 1938)	*Megacrania tsudai* (Phasmida, winged) (Maki, 1935)	*Carausius morosus** (Phasmida wingless) (Jeziorski, 1918)	*Australophasma coledonensis* (Mantophasmatodea wingless) Wipfler *et al* (2015)
IItpm10	+	-	IIpm7	48	-	+	-	?
IItpm11	-	-	-	-	-	-	-	-
IItpm12	-	-	-	-	-	-	-	-
IIppm1	-	-	IIpm5d+e	-	-	+	+	-
IIppm2	-	-	-	-	-	-	-	-
IIspm1	-	-	IIpm14	49	39	+	-	+
IIspm2	+	40	Iizm	50	40	+	+	+
IIspm3	-	61	Iiifm?	-	-	+	+	+
IIspm4	-		Iiifm?	-	-	-	-	-
IIspm5	-	-	-	-	-	-	-	+
IIspm6	+	-	-	-	-	-	-	-
IIspm7	+ ?	-	-	-	-	-	-	-
IIspm8	-	-	-	-	-	-	-	-
IIpcm1	+	53	IIpm5b+c	61	51	+	?	-
IIpcm2	+	42, (53)	IIpm1, IIpm2	61	51	+	+	-
IIpcm3	+	51, 52	IIpm4, IIpm5a	59, 60	49, 50	+	-	+
IIpcm4	+	(52)	(IIpm5a)	60	50	+	?	+
IIpcm5	+	55	IIpm3	-	-	+	+	+
IIpcm6	-	-	-	-	-	-	-	-
IIvlm1	-	35	-	-	-	+	-	-
IIvlm2	-	-	-	-	-	-	-	-
IIvlm3	+	59	IIvlm4, IIvlm5	67	-	-	-	+
IIvlm4	-	-	-	-	-	-	-	-
IIvlm5	+	60	IIvlm3	68	-	+	+	+
IIvlm6	-	-	-	-	-	-	-	-
IIvlm7	-	-	-	-	-	-	-	-
IIscm1	+ (2x)	44	IIbm1 (tripartite)	52	42	+	+	+
IIscm2	-	49	IIbm2	56	47	+	+	-

Additional File 2. Thoracic muscles of different representatives of Polyneoptera homologized following nomenclature by (Friedrich & Beutel 2008). *(continued)*

		Homologization by author					Homologization by Wipfler *et al* (2015)		
	species / muscle (Friedrich & Beutel, 2008)	*Troglophilus neglectus* (Rhaphidophoridae) (present study)	*Conocephalus maculatus* * (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus** (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides** (Caelifera, winged) (Maki, 1938)	*Atractomorpha sinensis** (Caelifera, macropterous) (Maki, 1938)	*Megacrania tsudai* (Phasmida, winged) (Maki, 1935)	*Carausius morosus** (Phasmida wingless) (Jeziorski, 1918)	*Austrophasma caledonensis* (Mantophasmatodea wingless) Wipfler *et al* (2015)
	IIscm3	+	50	IIbm3, IIbm6	57	48	?	+	+
	IIscm4	+	-	IIbm5	-	-	-	-	+
	IIscm5	+	48	IIbm7	-	46	-	-	+
	IIscm6	+	56	IIbm4	63	54	-	-	+
	IIscm7	+	68	IIvlm2	81	-	-	-	+
METATHORAX	IIIdlm1	+	58	IIIdlm1	66	57, 58?	-	-	+
	IIIdlm2	-	-	IIIdlm1a, IIIdlm3, IIIdlm4	-	-	+	-	+
	IIIdvm1	-	-	-	71	60	-	-	-
	IIIdvm2	+	66	IIIdvm1, IIIdvm6	80	67	?	-	+
	IIIdvm3	-	-	-	-	-	+	-	?
	IIIdvm4	+	70	IIIdvm3, IIIdvm4	84, 85	70	+	+	-
	IIIdvm5	+	71	IIIdvm2	86	71	+	+	+
	IIIdvm6	+	72	IIIpm6	87	72	+	+	+
	IIIdvm7	+	79	IIIdvm5	95, 96	79, 80	+	+	+
	IIIdvm8	-	-	IIIism	72	61	+	+	-
	IIItpm1	-	-	IIIpm10, IIIpm8?	73	-	?	-	+
	IIItpm2	-	62	IIIpm11	74	-	-	-	+
	IIItpm3	-	-	-	-	-	+	-	+
	IIItpm4	-	-	-	-	-	+	-	+
	IIItpm5	-	-	IIIpm9	75	-	+	-	+
	IIItpm6	-	-	-	-	-	+	-	-
	IIItpm7	-	-	-	-	-	-	-	-
	IIItpm8	-	-	IIIpm8?	-	-	-	-	-
	IIItpm9	-	63	IIIpm12	76	62, 63	+	-	-
	IIItpm10	+	64	IIIpm7	-		+	-	?
	IIItpm11	-	-	-			-	-	-
	IIItpm12	-	-	-			-	-	-

Additional File 2. Thoracic muscles of different representatives of Polyneoptera homologized following nomenclature by (Friedrich & Beutel 2008). *(continued)*

	Homologization by author					Homologization by Wipfler *et al* (2015)		
species / muscle (Friedrich & Beutel, 2008)	*Troglophilus neglectus* (Rhaphidophoridae) (present study)	*Conocephalus maculatus** (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus** (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides ** (Caelifera, winged) (Maki, 1938)	*Atractomorpha sinensis ** (Caelifera, macropterous) (Maki, 1938)	*Megacrania tsudai* (Phasmida, winged) (Maki, 1935)	*Carausius morosus** (Phasmida wingless) (Jeziorski, 1918)	*Austrophasma caledonensis* (Mantophasmatodea wingless) Wipfler *et al* (2015)
IIIspm1	-	-	-	77, 78	64, 65	+	-	+
IIIspm2	+	65	IIIzm	79	66	+	+	+
IIIspm3	+?	-	-			-	-	-
IIIspm4	-	-	-			-	-	-
IIIspm5	+?	-	-			-	-	+
IIIpcm1	+	78	IIIpm5b	78	94	-	+	-
IIIpcm2	+	67, (78)	IIIpm1, IIIpm2	78	94	+	+	-
IIIpcm3	+	76, 77	IIIpm4	76, 77	92, 93	+	-	+
IIIpcm4	+	(77)	IIIpm5a	77	93	+	?	+
IIIpcm5	+	80	IIIpm3	-	-	-	+	+
IIIpcm6	-	-	-			-	-	-
IIIpcm7	-	-	-			-	-	-
IIIvlm1	-	-	-	70	59	+	-	-
IIIvlm2	-	88?	IIIvlm2-5	104?	87?	-	+	+
IIIvlm3	-	85?	IIIvlm1	103?	86?	-	-	-
IIIscm1	+	69	IIIbm1	82, 83	68, 69	+	+	+
IIIscm2	+	73	IIIbm2	88	73	+	+	-
IIIscm3	+	75	IIIbm3	90, 91	75	?	+	+
IIIscm4	+	74	IIIbm5	89	74	-	-	+
IIIscm5	-	-	-			-	-	+
IIIscm6	+	81	IIIbm4	97	81	+	+	+

Chapter 2

The thoracic morphology of the wingless dune cricket *Comicus calcaris* (Orthoptera: Schizodactylidae): novel apomorphic characters for the group and adaptations to sand desert environments

Fanny Leubner, Sven Bradler, Benjamin Wipfler

published in: Arthropod Structure & Development

Leubner, F., Bradler, S., Wipfler, B. 2017. The thoracic morphology of the wingless dune cricket *Comicus calcaris* (Orthoptera: Schizodactylidae): novel apomorphic characters for the group and adaptations to sand desert environments. *Arthropod Structure & Development*, 46, 449–461. DOI: 10.1016/j.asd.2017.03.006.

Abstract

Schizodactylidae, splay-footed or dune crickets, represents a distinct lineage among the highly diverse orthopteran subgroup Ensifera (crickets, katydids and allies). Only two extant genera belong to the Schizodactylidae: the winged Eurasian genus *Schizodactylus*, whose ecology and morphology is well documented, and the wingless South African *Comicu*s, for which hardly any studies providing morphological descriptions have been conducted since its taxonomic description in 1888.

Based on the first in-depths study of the skeletomuscular system of the thorax of *Comicus calcaris* Irish 1986, we provide information on some unique characteristics of this character complex in Schizodactylidae. They include a rigid connection of prospinasternite and mesosternum, a T-shaped mesospina, and a fused meso- and metasternum. Although Schizodactylidae is mainly characterized by group-specific anatomical traits of the thorax, its bifurcated profuca supports a closer relationship to the tettigonioid ensiferans, like katydids, wetas, and hump-winged crickets. Some specific features of the thoracic musculature of *Comicus* seem to be correlated to the skeletal morphology, e.g. due to the rigid connection of the tergites and pleurites in the pterothorax not a single direct flight muscle is developed. We show that many of the thoracic adaptations in these insects are directly related to their psammophilous way of life. These include a characteristic setation of thoracic sclerites that prevent sand grain from the intrusion into vulnerable membranous areas, the striking decrease in size of the thoracic spiracles that reduces the respirational water loss, and a general trend towards a fusion of sclerites in the thorax.

Keywords: Ensifera, sand crickets, splay-footed crickets, psammophilous life, *Schizodactylus*

Introduction

Schizodactylidae forms one of the most peculiar taxa within the highly diverse long-horned grasshoppers (Ensifera: crickets, katydids and allies). As these insects exclusively inhabit sand dune areas (Irish 1986; Aydin & Khomutov 2008; Channa *et al.* 2013), and are characterized by broad lobe-like tarsal expansions, they are commonly referred to as splay-footed, dune or sand crickets (Khattar 1972a; Kevan 1982). In the fossil record, Schizodactylidae is documented since the Lower Cretaceous, although this lineage may be considerably older (Heads & Leuzinger 2011). They are considered to be a relict group, comprising merely 15 extant species (Eades *et al.* 2015) and only two extant genera, *Schizodactylus* and *Comicus* (Kevan 1982) with a disjunct distribution pattern. The winged genus *Schizodactylus* is mainly distributed in India, Pakistan, Sri Lanka and Myanmar (Khattar 1972a; Channa *et al.* 2013), only the brachypterous *Schizodactylus inexpectatus* is endemic in Turkey (Aydin 2005). In contrast, the wingless genus *Comicus* is restricted to southern regions in Africa (Irish 1986). Both, *Comicus* and *Schizodactylus* exclusively live in sand dune areas (Irish 1986; Aydin 2005; Channa *et al.* 2013). Sand dunes form unique habitats due to the constantly changing structure driven by poor vegetation and strong winds (Aydin & Khomutov 2008). *Schizodactylus* inhabits shifting or fixed sand dune systems and shows a comparatively low tolerance against drought (Khattar 1972a; Aydin & Khomutov 2008). *Comicus* is restricted to desert habitats of the Namib and Kalahari (Irish 1986). In addition to their exclusive habitat, members of the Schizodactylidae have a characteristic burrowing behavior, resting in their burrows at day and being active at night (Ramme 1931; Channa *et al.* 2013). The monophyly of Schizodactylidae is supported by unique morphological traits, e.g. tarsal morphology, absence or drastic reduction of external genitalia, and thickened tibiae (Ander 1939), and has been confirmed in a recent molecular phylogeny of ensiferans, the first to include both genera of the taxon (Song *et al.* 2015). The systematic placement of Schizodactylidae within the Ensifera still remains inconsistent and the group was placed with either of the two main ensiferan subgroups: the 'grylloid clade' including crickets and mole-crickets (Ragge 1955; Gwynne 1995; Jost & Shaw 2006) or the 'tettigonioid clade' including cave crickets, raspy crickets, Jerusalem crickets, wetas and katydids (Ander 1939; Desutter-Grandcolas 2003; Song *et al.* 2015). Several studies deal with the general morphology (Khattar 1960, 1972a,b; Khattar &

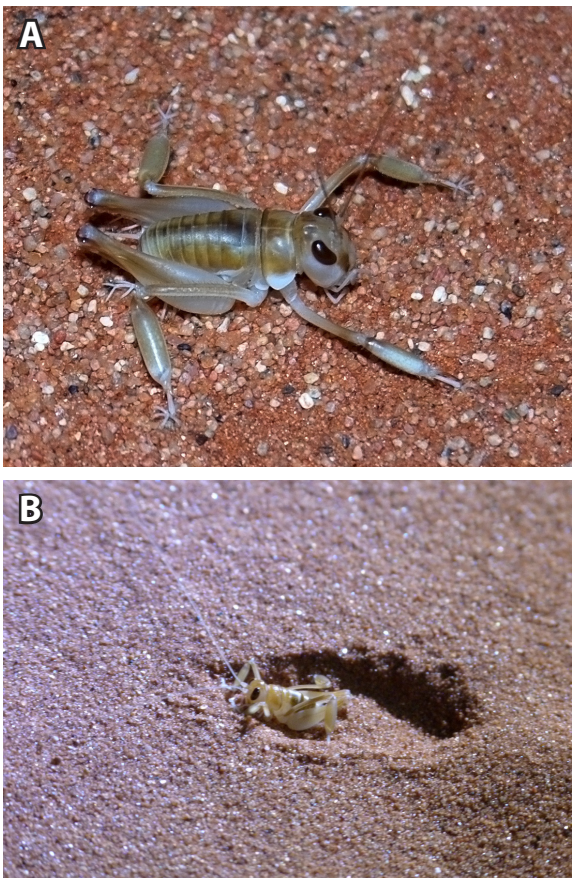


Figure 1. *Comicus calcaris* in its natural habitat, the Namib desert. (A) Close-up image showing characteristic tarsal broadenings. (B) Resting in its self-burrowed pit.

Srivastava 1962) and ecology (Aydin & Khomutov 2008; Channa *et al.* 2013) of the Eurasian genus *Schizodactylus*. Mainly due to the presence of wings in *Schizodactylus*, only this genus was considered in ensiferan taxonomy studies that were based on wings and wing venation in particular (Zeuner 1939; Ragge 1955; Sharov 1968) and, resulting from that, included in cladistic analyses of morphological characters (Gwynne 1995; Desutter-Grandcolas 2003). In contrast, only little is known about the morphology of the South African genus *Comicus* (Irish 1986).

The present study aims on filling this gap by providing the first detailed description of the skeletomuscular system of the thorax of the wingless schizodactylid *Comicus calcaris* Irish 1986 (Fig.1). The thoracic musculature of *Comicus* is homologized to the nomenclature established by Friedrich & Beutel (2008) and - based on this homologization - thoroughly compared to the musculature found in other representatives of Orthoptera. Secondary winglessness is accompanied by specific modifications of the thoracic musculature (Leubner et al. 2016), and we will look for comparable adaptive changes in *Comicus* in particular. Furthermore, we examined the thoracic skeletal system and associated structures of *Comicus* and *Schizodactylus* (Khattar 1960, 1972a; Khattar & Srivastava 1962) for potential apomorphic traits for Schizodactylidae and specific adaptations towards a life in sand dunes.

Material & Methods

The specimens of *Comicus calcaris* Irish 1986 were collected in February 2012 on a sand dune behind the Gunsbeweys-Farm in Namibia (S26° 10.761', E16° 21.592', elevation of 1007 m). All investigated specimens were preserved in 70% ethanol. We exclusively investigated female specimens to ensure a maximum comparability with other studies on the ensiferan thorax. In total, three specimens were used and prepared for differing investigation methods. One specimen was cut sagittally and macerated in 5% KOH (1 hour in a heating cabinet with 60°C) to remove interior soft tissues. It was subsequently dried using the HMDS (Hexamethyldisilazane, Carl Roth GmbH & Co KG, item number 3840.2) procedure (Friedrich *et al.* 2013). Photographs were taken using a Nikon D 90 digital SLR equipped with a 40-mm and with a 63- mm Zeiss Luminar macro lens, plus an adjustable extension bellow. The specimen was illuminated by two flashlights fitted with a transparent cylinder for even and soft light. Helicon Focus Mac Pro X64 was used to combine a stack of several partially focused images. The same specimen was utilized to prepare drawings of the thoracic sclerites including membranous areas using a *camera lucida* on a stereomicroscope ZEISS Stemi SV11. One specimen was dehydrated in a graded ethanol series and dried at the critical point (Balzer CPD 030). The dry specimen was sputter-coated with gold (Balzer SCD050 sputter coater). Pictures were taken with a Philips XL 30 ESEM (applied voltage: 10 kV) and Scandium software. In order to investigate the thoracic musculature, another specimen was dehydrated in a graded ethanol series, critical-point dried (Balzer CPD 030) and mounted on a specimen holder (aluminium stub). The µ-computed tomography (µ-CT) scan was performed at the Deutsches Elektronen Synchrotron (DESY, Hamburg, Germany) with an energy of 8 keV (3 different scan levels; rotation: 180° in steps of 0.25°; spatial resolution: 4.8 µm) . The µ-CT scan was imported in AMIRA® 5.4.3 (Visage Imaging, Berlin, Germany) for segmentation. Each segmented material was separated with the algorhythm function of Amira and subsequently imported into VG Studio Max 2.0.5 (Volume Graphics, Heidelberg, Germany) for volume rendering (Scatter HQ). All figure plates were arranged using Adobe Illustrator® CS3.

The terminology of the thoracic skeleton largely follows Snodgrass (Snodgrass 1935), terms used by authors of ensiferan-specific literature (Voss 1905a; Snodgrass 1929; Ander

1939) are mentioned in case of inconsistency. The thoracic musculature of *C. calcaris* is described, and muscles are numbered consecutively. We homologize the observed muscles in *C. calcaris* following the nomenclature of Friedrich and Beutel (2008) to facilitate comparisons with results of other authors. Table S1 (supplementary information) compares the set of thoracic muscles found in *C. calcaris* with those of other ensiferan and a number of caeliferan taxa. The homology hypotheses for the thoracic musculature of other representatives of the Ensifera (Tettigoniidae: *Conocephalus maculatus* (Maki 1938) (*Xiphidion maculatum* therein); Gryllidae: *Acheta domesticus* (Voss 1905b) (*Gryllus domesticus* therein); Rhaphidophoridae: *Troglophilus neglectus* (Leubner *et al.* 2016)) and Caelifera (Acrididae: *Locusta migratoria migratorioides* (Maki 1938) (*Locusta manilensis* therein), *Locusta migratoria migratoria* (Albrecht 1953); Pyrgomorphidae: *Atractomorpha sinensis* (Maki 1938) (*Atractomorpha ambigua* therein) were taken from (Leubner *et al.* 2016). Additionally, the present study provides further homology hypotheses for the thoracic musculature of *Cephalocoema albrechti* (Proscopiidae) (de Zolessi 1968), *Dissosteira carolina* (Acrididae) (Snodgrass 1929) and an unspecified representative of the matchstick grasshoppers (Eumastacidae) (Blackith & Blackith 1967). The current taxonomy of the examined species follows Eades et al. (Eades *et al.* 2015). Hereafter, only the generic names are used for these species.

Results

Skeleton

The thorax of the examined females of *Comicus* measures 3 to 4 mm in length, corresponding to approximately one quarter of the total body length. The dorsal side of the thorax is much shorter than the ventral side. The diameter of the thorax increases from anterior to posterior. The pro- and pterothorax are approximately equal in length. The skeleton is of yellowish/sandy color (Figs. 1, 2A). *Comicus* entirely lacks wings and wing base sclerites. The phragmata are only weakly developed.

Prothorax

The head capsule is connected to the thorax by the cervical membrane. In vivo, this membrane is not exposed, the head is retracted and partly covered by the pronotum (Fig.

1A). The neck region bears a pair of lateral cervical sclerites on each body side. The first lateral cervical sclerite is arcuate and can be subdivided into three surface areas by orientation: an anterior **a1lcv**, a lateral **l1lcv** and a ventral surface **v1lcv** (Figs. 2B, 3A, 4D). The anterior surface is triangular and articulates with the postoccipital rim by a small condylus. Its internal median ridge is strongly sclerotized and possesses two apodemes that serve as attachment points for the cervical muscle m6. The ventral surface **v1lcv** forms an acute triangle, the sharpest angle oriented mesad. The anterior and ventral surfaces of the first cervical sclerite are connected by a laterally oriented triangular lateral surface **l1lcv**, which articulates with the second lateral cervical sclerite **2lcv**. The second lateral cervical sclerite is club-shaped. Its wide end articulates with the lateral surface of the first cervical sclerite, the posterior condylus interacts with the pleurosternal bridge **psb** (Figs. 2B, 3A, C,

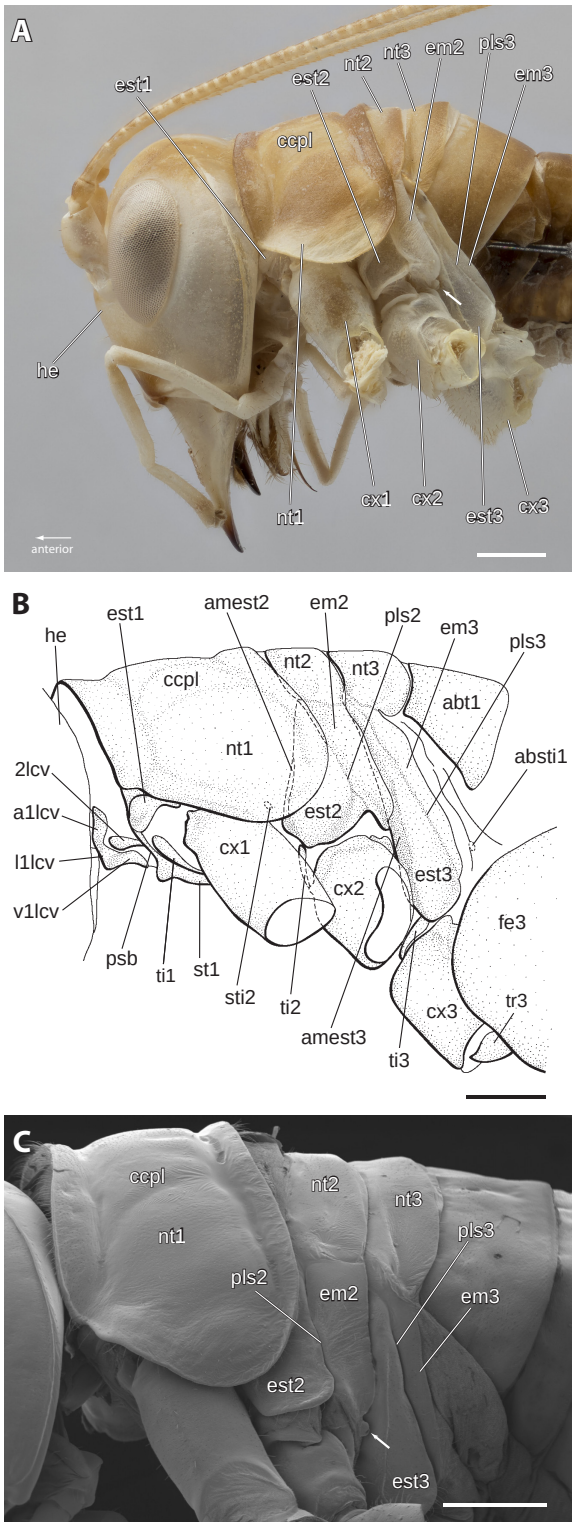
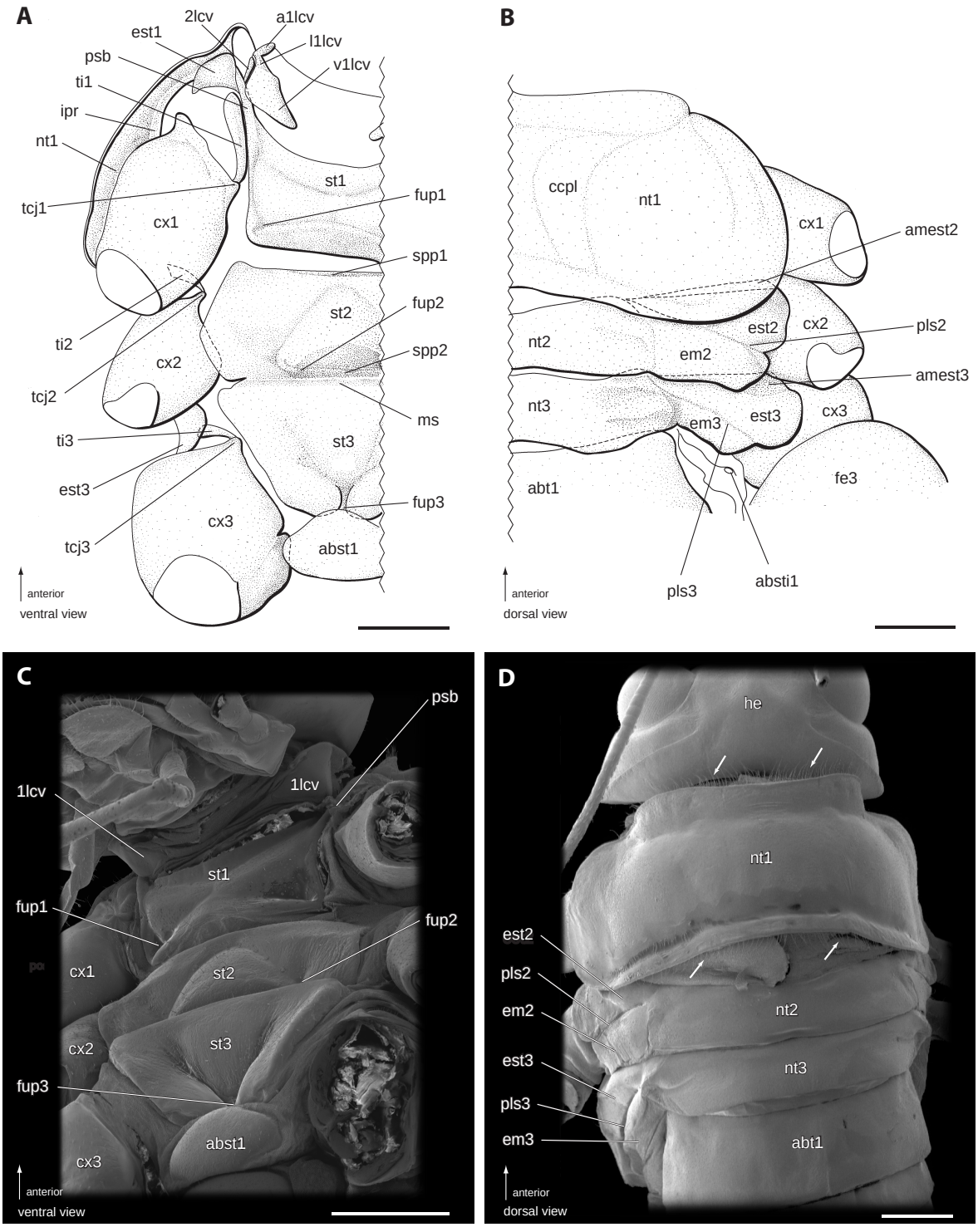


Figure 2. Thoracic skeleton of *Comicus calcaris*, exterior lateral view as (A) photograph, (B) drawing, (C) scanning electron micrograph. Right body half. Hidden structures in (B) shown as dashed lines, membranous parts blank. White arrow in (C) marks the exceedingly small metathoracic stigma. Abbreviations: *1/2lcv* 1st /2nd lateral cervical sclerite, *absti1* 1st abdominal stigma, *a1lcv* anterior surface of 1st cervical sclerite, *abt1* 1st abdominal tergum, *amest2/3* anterior margin of mes-/metepisternum, *ccpl* contact area of cryptopleura, *cx1/2/3* pro-/ meso-/ metacoxa, *em2/3* mes-/metepimeron, *est1/2/3* pro-/ mes-/metepisternum, *fe3* metafemur, *he* head, *l1lcv* lateral surface of 1st cervical sclerite, *nt1/2/3* pro-/ meso-/metanotum, *pls2/3* meso-/metathoracic pleural suture, *psb* pleurosternal bridge, *ti1/2/3* pro-/ meso-/metatrochantin, *tr3* metatrochanter, *st1* prosternum, *sti2* mesothoracic stigma, *v1lcv* ventral surface of 1st cervical sclerite. Scale bars: 1 mm.

4B; *precoxal bridge* in Snodgrass 1929, *Coxosternum* in Voss 1905a). The outer edges of the saddle-shaped pronotum **nt1** are strongly sclerotized (Fig. 2A). Dorsally, the anterior and posterior borders of the pronotum are covered by long setae (white arrows in Fig. 3D). The pronotal surface is roughly structured with the exception of a smooth-surfaced area, where the internally exposed cryptopleura contacts the pronotum from inside (**ccpl**; Figs. 2B, 3B). The membranous fold that connects the tergal and pleural skeletal elements of the prothorax, forms a hardly sclerotized ridge along the internal surface of the pronotum approximately at its lower third, termed as internal pronotal ridge **ipr** (Figs. 3A, 4D). Additionally, nearly the whole prothoracic pleuron is hidden by the pronotum, hence referred to as cryptopleura **cpl** (Fig. 4A, B, D; *Pleurallamelle* in Voss 1905a). Only a small, bulb-like part of the proepisternum **est1** is visible in an exterior view (Fig. 2). The cryptopleura, composed of the anterior expanded proepisternum and the posterior narrow proepimeron, is more or less sail-shaped (Fig. 4). The anterior part of the cryptopleura, the proepisternum, is situated anterior to the pleural ridge **plr1** (Fig. 4D). From a median view, the cryptopleura is concave in the lower two thirds having the shape of a semicircular tube (Fig. 4A, D). The proepimeron is merely a small area posterior to the propleural ridge. The propleural ridge **plr1** is well developed and forms the pleurocoxal articulation **pcj1** at its ventral tip with the lateral procoxal rim **cxr1** (Fig. 4D). A propleural arm is absent. The slender prothoracic trochantin **ti1** is embedded in the coxal corium and articulates with the procoxa at its anteromedian border by the trochantinocoxal joint **tcj1** (Fig. 3A). The anterior ventral edge of the proepisternum passes into the pleurosternal bridge **psb** that connects the cryptopleura with the prosternum **st1** (Figs. 2B, 3A, C, 4B, D). The prosternum is of nearly rectangular shape (Fig. 3A, C). Its outer surface is characterized by paired raised

Figure 3 (see opposite page). Thoracic skeleton of *Comicus calcaris*, (A) and (C) ventral view, (B) and (D) dorsal view. (A), (B) Drawings of right body half, hidden structures shown as dashed lines, membranous parts blank. (C), (D) Scanning electron micrographs. White arrows in (D) mark the long setae at anterior and posterior margins of the pronotum. Abbreviations: *1/2lcv* 1st /2nd lateral cervical sclerite, *a1lcv* anterior surface of 1st cervical sclerite, *abst1* 1st abdominal sternum, *absti1* 1st abdominal stigma, *abt1* 1st abdominal tergum, *ccpl* contact area of cryptopleura, *cx1/2/3* pro-/ meso-/ metacoxa, *em2/3* mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fe3* metafemur, *fup1/2/3* furcal pit of pro-/meso-/metathorax, *he* head, *ipr* inner pronotal ridge, *l1lcv* lateral surface of 1st cervical sclerite, *ms* median sclerite, *nt1/2/3* pro-/meso-/metanotum, *pls2/3* meso-/metathoracic pleural suture, *psb* pleurosternal bridge, *spp1/2* pro-/mesospinal pit, *st1/2/3* pro-/meso-/metasternum, *tcj1/2/3* trochantino-coxal joint of pro-/meso-/metathorax, *ti1/2/3* pro-/meso-/metatrochantin, *v1lcv* ventral surface of 1st cervical sclerite. Scale bars: 1mm.

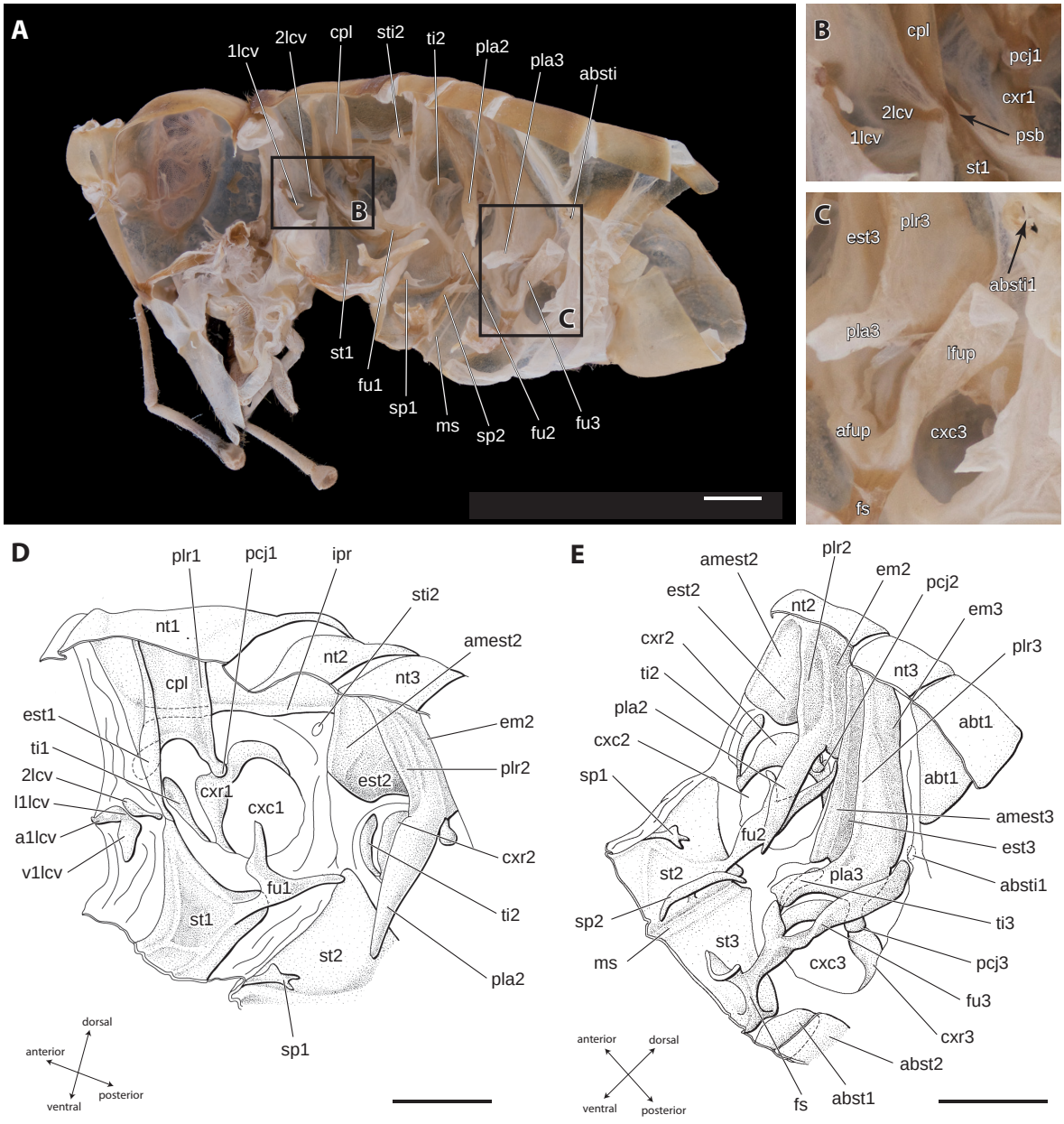
areas, delimited by distinct grooves (Fig. 3A, C). These nearly trapezoid areas adjoin each other at their shorter edge in the median region of the prosternum (Fig. 3A, C). The furcal pits **fup1** are situated at the posterolateral corners of the prosternum (Fig. 3A, C) and bear an internal protrusion on both sides, the profurca **fu1** (Fig. 4A, D). Each profurcal arm is



bifurcated, one ramus projecting in an anterior, the other in a posterolateral direction (Fig. 4A, D). A separated and distinct prospinasternite is not present; the prospina **sp1** arises medially from the anterior margin of the mesosternum (Figs. 3A, B, 4A, D). It bears three processes: an unpaired anterior one, and paired posterolateral ones (Fig. 4D).

Mesothorax

The mesothorax is the narrowest segment of the thorax. The uniform mesonotum **nt2** is not divided in substructures by sutures or grooves (Figs. 2, 3B, D). The mesonotum is not



separated from the mesothoracic pleura by a membranous area; instead, a narrow ridge is present between both elements (Figs. 2, 3D). The mesothoracic pleuron consists of an anterior episternum **est2** and a posterior epimeron **em2** (Fig. 2). The mesepisternum is triangular, its broad basis situated at the ventral margin (Fig. 2). It is characterized by an anterior margin **amest2**, a triangular area that extends mesad (Figs. 2, 3B, 4E). The mesepimeron is rectangular and its dorsal edge fits close to the lateral edge of the mesonotum (Fig. 3B). Both parts of the pleura, episternum and epimeron, are separated by the deep pleural suture **pls2**, which is oriented slightly diagonal to the dorso-ventral body axis (Fig. 2). The pleural suture ends approximately at the level of the anterolateral corner of the mesonotum (Figs. 2, 3B). Internally, the pleural suture forms the pleural ridge **plr2** that extends medially into the tapered mesopleural arm **pla2** (Fig. 4A, E). The pleurocoxal joint **pcj2** is situated at the ventral edge of the mesothoracic pleura at the level of the pleural ridge (Fig. 4E). The slender and sickle-shaped mesothoracic trochantin **ti2** articulates anteroventrally with the mesothoracic coxal rim **cxr2** via the trochantinocoxal joint **tcj2** (Figs. 3A). The meso- and metathoracic sterna, **st2** and **st3**, form a single composite sclerite. At its posterior edge, the mesothoracic sternum is connected to the anterior edge of the metasternum by a narrow median sclerite **ms** that is separated to both sclerites by sutures (Fig. 3A; definition follows Ander 1939, *Mediansklerit* therein). The mesosternum is nearly rectangular and about twice as wide as long (Fig. 3A, C). Medially, the mesosternum bears a raised equilateral triangular area that is separated by deep grooves (Fig. 3A, C). The two furcal pits **fup2** at its posteriolateral corners (Fig. 3A, C) bear the internally located mesofurca **fu2** (Fig. 4A, E). Each bifurcated furcal arm extends laterally onto the level of the coxal cavity **cxc2** and bears

Figure 4 (see opposite page). Thoracic skeleton of *Comicus calcaris*, interior lateral view of right body half as (A)–(C) photographs, (D)–(E) drawings, hidden structures shown as dashed lines, membranous parts blank. The illustrations are shifted along the anterior-posterior-axis to visualize relevant details of the exoskeleton. (A) overview, (B) detail of sternopleural area of prothorax, (C) detail of sternopleural area of metathorax, (D) neck region and prothoracic exoskeleton, (E) meso- and metathoracic exoskeleton. Abbreviations: *1/2lcv* 1st /2nd lateral cervical sclerite, *abst1/2* 1st/2nd abdominal sternum, *absti1* 1st abdominal stigma, *a1lcv* anterior surface of 1st cervical sclerite, *abt1* 1st abdominal tergum, *afup* anterior furcal process, *amest2/3* anterior margin of mes-/metepisternum, *cpl* cryptopleura, *cxc1/2/3* coxal cavity of pro-/meso-/metathorax, *cxr1/2/3* coxal rim of pro-/meso-/metathorax, *em2/3* mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fs* furcal stem, *fu1/2/3* pro-/meso-/metafurca, *ipr* inner pronotal ridge, *l1lcv* lateral surface of 1st cervical sclerite, *lfup* lateral furcal process, *ms* median sclerite, *nt1/2/3* pro-/meso-/metanotum, *pcj1/2/3* pleuro-coxal joint of pro-/meso-/metathorax, *pla2/3* meso-/metathoracic pleural arm, *plr1/2/3* pro-/meso-/metathoracic pleural ridge, *psb* pleurosternal bridge, *ti1/2/3* pro-/meso-/metatrochantin, *sp1/2* pro-/mesopina, *st1/2/3* pro-/meso-/metasternum, *sti2* mesothoracic stigma, *v1lcv* ventral surface of 1st cervical sclerite. Scale bars: 1 mm.

an anterior and a posterolateral process (Fig. 4E). The mesothoracic pleural arm and the adjacent posterolateral process of the mesofurca run close to each other along a horizontal axis (Fig. 4E). The single spinal pit **ssp2** lies medially between the two furcal pits (Fig. 3A). The spina **sp2** is situated medially between the furcal stems of each body half (Fig. 4E). It is T-shaped, bearing a short stem and a broad slightly curved bar that is oriented transversally to the longitudinal body axis (Fig. 4E). The meso- and metathoracic pleural sclerites are closely adjacent, with no membranous part observable between them. At the posterior end of the internal pronotal ridge **ipr**, the circular mesothoracic stigma **sti2** is embedded in the intersegmental membrane and covered by the ventrally elongated pronotum (Figs. 2B, 4A, D).

Metathorax

Similar to the mesonotum, the metanotum **nt3** is not subdivided by ridges or sutures (Figs. 2, 3B, D). As it is the case in the mesothorax, the metanotum and the metathoracic pleura are not separated from each other by a thin membrane, but a shallow ridge is present between both parts (Figs. 2, 3B). The metapleural sclerites are narrower than their mesothoracic counterparts (Fig. 2). The deep pleural suture **pls3** divides the metathoracic pleura into an anterior episternum **est3** and a posterior epimeron **em3** (Fig. 2). The anterior margin of the metathoracic episternum **amest3** is considerably narrower than the mesothoracic one (Fig. 4E). Internally, the metathoracic pleural suture forms a distinct pleural ridge **plr3** that extends medially into the long pleural arm **pla3**. In contrast to the mesothoracic pleural arm, the metathoracic one ends in an obtuse apex (Fig. 4C, E). The first abdominal stigma **absti1** is situated in the lower third of the membranous area posterior to the narrow metathoracic epimeron (Figs. 2, 3B). The voluminous metacoxa **cx3** articulates with the pleura via the pleurocoxal joint **pcj3** (Fig. 4) and, in addition, with the slender sickle-shaped trochantin **ti3** via the trochantinocoxal joint **tcj3** (Fig. 3A). The metathoracic sternum **st3** is of trapezoidal shape and anteriorly fused with the mesosternum. A distinct furcasternum is not present. The anterior edge of the metasternum is as wide as the posterior edge of the mesosternum (Fig. 3B, D). Posteriorly, the metasternum becomes narrower, and terminates medially in a single furcal pit **fup3** (Fig. 3B, D). The metafurca **fu3** has a single short common stem **fs** and extends laterally into the bifurcated furcal arms (Fig. 4C, E). As in the mesothorax, each metafurcal arm has an anterior and a posterolateral process, the latter directly projecting

beneath the pleural arm (Fig. 4C, E). A metathoracic spina is lacking. The metathoracic stigma, situated between the pleurites of the meso- and metathorax is exceedingly small (Fig. 2A) and could be observed more easily through scanning electron microscopic inspection (Fig. 2C).

Musculature

In total, 69 thoracic muscles were identified (28 prothoracic, 21 mesothoracic, and 20 metathoracic muscles). All thoracic muscles of *Comicus* are illustrated in figure 5. A detailed description of these muscles is provided in table 1 containing origin, insertion and specific characteristics, as well as referring to the corresponding illustration in figure 5. In addition, table 1 provides a hypothesis for the homology of the muscles of *Comicus* with the muscles generally reported from neopteran insects (Friedrich & Beutel 2008).

Table 1. Thoracic muscles of *Comicus calcaris*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the present study. Furthermore, a proposed homologization (Hom*) according to the nomenclature after Friedrich & Beutel (2008) is provided.

Present study	Hom*	Origin	Insertion	Remarks	Figure
PROTHORAX					
Dorsal longitudinal muscles					
1	Idlm1	median region of prophragma	dorsal area of occipitale (close to m2)		5B
2	Idlm2	near posteromedian margin of pronotum	dorsal area of occipitale (ventral to m1)		5A
3	Idlm5	dorsomedial on pronotum	median region of prophragma (close to m1)		5C
4	Idlm6	posteriomedial on pronotum	dorsolateral part of prophragma		5E
Dorsoventral muscles					
5	Idvm2, Idvm3?	posterior part of first lateral cervical sclerite	dorsolateral area of occipitale		5C, E
6	Idvm4?	dorsolateral at anterior margin of pronotum	anterior part of first lateral cervical sclerite		5B, C
7	Idvm9	tip of anterior ramus of profurca	dorsolateral area of occipitale (close to m5)	strong	5F
8	Idvm10	dorsal face of anterior ramus of profurca	ventral area of prophragma		5B
9	Idvm13	posterior dorsolateral area ofpronotum (posterior to cryptopleura)	prothoracic trochantin near trochantino-coxal joint		5C
10	Idvm16	medial region of pronotum	posterior procoxal rim	long thin tendon	5D
11	Idvm17	posterior region of pronotum	posterior procoxal rim (close to m12)	fanned out	5F
12	Idvm18	posterior region of pronotum	posterolateral procoxal rim (close to pleuro-coxal joint)	fanned out	5F
13	Idvm19	lateral area of pronotum	trochanter (with m19)		5E

Table 1. Thoracic muscles of *Comicus calcaris*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the present study. Furthermore, a proposed homologization (Hom*) according to the nomenclature after Friedrich & Beutel (2008) is provided. *(continued)*

Present study	Hom*	Origin	Insertion	Remarks	Figure
Tergopleural muscles					
14	Itpm2-1	laterally on cervical membrane	anteriolateral area of cryptopleura (on outer surface)	short	5E, F
15	Itpm2-2	laterally on cervical membrane (close to m14)	anterodorsal margin of cryptopleura		5E
Pleurocoxal muscles					
16	Ipcm3	anterodorsal region of cryptopleura (on inner surface)	prothoracic trochantin		5C
17	Ipcm4	anterodorsal area of cryptopleura (on inner surface)	anterior coxal rim		5E
18	Ipcm5	posterodorsal area of cryptopleura (on inner surface)	anterior procoxal rim (close to pleuro-coxal joint)		5D
19	Ipcm8	anterodorsal and posterodorsal area of cryptopleura (on inner surface)	trochanter (with m13)	2 bundles (on episternum and epimeron)	5D
Ventral longitudinal muscles					
20	Ivlm3	ventral surface of posterior ramus of profurca	ventral area of occipitale		5B
21	Ivlm4	ventral tip of posterior ramus of profurca	prospina		5B
22	Ivlm6	base of posterior ramus of profurca	anterior face of posterolateral process of prospina		5C
23	Ivlm7-1	posterior face of profurcal stem	anterior arm of mesofurca		5D
24	Ivlm7-2	posterior face of profurcal stem (dorsal of m23)	anterior arm of mesofurca (median of m23)		5D
Sternocoxal muscles					
25	Iscm1	lateral face of profurca stem	anterior procoxal rim		5D
26	Iscm2	lateral face of anterior ramus of profurca	posterior procoxal rim		5F
27	Iscm3	ventral face of anterior ramus of profurca	mesal procoxal rim		5E
28	Iscm4	lateral face of posterior ramus of profurca	lateral procoxal rim		5B
MESOTHORAX					
Dorsal longitudinal muscles					
29	IIdlm1	several indistinct bundles covering median region of prophragma	median region of mesophragma	muscular coating	5D
Dorsoventral muscles					
30	IIdvm4, IIdvm5	central region of mesonotum	posterior mesocoxal rim	long thin tendon	5C
31	IIdvm6	posterolateral mesocoxal rim	dorsal edge of mesepimeron		5C
32	IIdvm7	anterior region of mesonotum	trochanter (with m40 and m48)		5B
33	IIdvm8	dorsal face of posterior arm of mesofurca	ventrolateral area of mesonotum	slender	5C
Pleuropleural muscles					
34	IIppm1	ventral part of anterior margin of mesepisternum	intersegmental membrane between pro- and mesothorax	slender	5E
Sternopleural muscles					
35	IIspm2	dorsal surface of mesofurca	ventral surface of mesopleural arm		5E

Table 1. Thoracic muscles of *Comicus calcaris*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the present study. Furthermore, a proposed homologization (Hom*) according to the nomenclature after Friedrich & Beutel (2008) is provided. *(continued)*

Present study	Hom*	Origin	Insertion	Remarks	Figure
Pleurocoxal muscles					
36	IIpcm1	ventral part of anterior margin of mesepisternum	mesothoracic trochantin		5E
37	IIpcm2	inner anteroventral and anterodorsal part of anterior margin of mesepisternum	anterior mesocoxal rim	one short, one long bundle	5D, E
38	IIpcm3	inner anterodorsal part of anterior margin of mesepisternum (between bundles of m37)	anterolateral mesocoxal rim		5E
39	IIpcm4	dorsal and ventrolateral part of mesepisternum (near mesopleural ridge)	anterolateral mesocoxal rim (close to m38)	2 bundles (one very short)	5E
40	IIpcm5	dorsal part of mesepisternum (dorsad of m39)	trochanter (with m32 and m48)		5D
Ventral longitudinal muscles					
41	IIvlm3	posterior arm of mesofurca (near stem)	tip of anterior arm of metafurca		5C
42	IIvlm5	posterior face of of mesospina	anterior arm of metafurca (near furcal stem)		5A, B
Sternocoxal muscles					
43	IIscm1-1	laterally on mesofurca (near stem)	anterior mesocoxal rim		5D
44	IIscm1-2	laterally on sternal edge of mesofurcal stem	anterior mesocoxal rim (close to m43)		5B
45	IIscm3	ventral face of mesofurca	mesal mesocoxal rim		5F
46	IIscm4	ventral face of mesofurca (posterior to m45)	lateral mesocoxal rim (close to pleuro-coxal joint)		5C
47	IIscm5	tip of lateral process of mesospina	posterior mesocoxal rim		5E
48	IIscm6	ventral face of mesofurca (laterad to m45 and m46)	trochanter (with m32 and m40)		5F
49	IIscm7	tip of lateral process of mesospina	anteriolateral metacoxal rim		5D
METATHORAX					
Dorsal longitudinal muscles					
50	IIIdlm1	several indistinct bundles covering median region of mesophragma	median region of metaphragma	muscular coating	5D
Dorsoventral muscles					
51	IIIdvm2	mesophragma and anterior part of metanotum	metathoracic trochantin		5C
52	IIIdvm4, IIIdvm5	central region of metanotum	posterior metacoxal rim		5C
53	IIIdvm6	posterior metacoxal rim	dorsal edge of metepimeron		5D
54	IIIdvm7	central region of metanotum (ventrad to m52)	trochanter (with m64 and m69)		5D
55	IIIdvm8	dorsal face of posterolateral arm of metafurca	membrane below ventrolateral area of metanotum	stronger than mesothoracic homologue (m33)	5B
Pleuropleural muscles					
56	IIIppm1	ventral part of anterior margin of metepisternum	intersegmental membrane between meso- and metathorax		5E

Table 1. Thoracic muscles of *Comicus calcaris*, specifying origin and insertion of each muscle including noteworthy characteristics and corresponding figure in the present study. Furthermore, a proposed homologization (Hom*) according to the nomenclature after Friedrich & Beutel (2008) is provided. *(continued)*

Present study	Hom*	Origin	Insertion	Remarks	Figure
Sternopleural muscles					
57	IIIspm2	dorsal surface of metafurca	ventral surface of metapleural arm		5E
58	IIIspm5-1?	posterior edge of metasternum near metafurcal stem	intersegmental membrane between metathorax and abdominal pleura		5A, B
59	IIIspm5-2	posterior face of posterolateral arm of metafurca	intersegmental membrane between metathorax and abdominal pleura (laterad to 58)		5A, B
Pleurocoxal muscles					
60	IIIpcm1	dorsal part of metepisternum	metathoracic trochantin		5D
61	IIIpcm2	inner anterodorsal part of anterior margin of metepisternum	anterior metacoxal rim		5E
62	IIIpcm3	posterodorsal part of metepisternum	lateral metacoxal rim		5F
63	IIIpcm4	ventral part of metepisternum (near metapleural ridge)	lateral metacoxal rim (close to m62)		5F
64	IIIpcm5	dorsal part of metepisternum (dorsad of m61)	trochanter (with m54 and m69)		E
Sternocoxal muscles					
65	IIIscm1	laterally on metafurcal stem	anterior metacoxal rim		5C
66	IIIscm2	posteroventral face of metafurcal arm and common stem	posterior metacoxal rim		5A, B
67	IIIscm3	ventral face of posterolateral arm of metafurca	mesal metacoxal rim		5C
68	IIIscm4	tip of posterior posterolateral arm of metafurca	lateral metacoxal rim		5C
69	IIIscm6	tip of anterior posterolateral arm of metafurcal	trochanter (with m54 und m64)		5D

Discussion

The thoracic morphology of Schizodactylidae: autapomorphies and phylogenetic implications

Both genera of the Schizodactylidae, *Comicus* (this study) and *Schizodactylus* (Khattar 1960; Khattar & Srivastava 1962), show characteristics in thoracic morphology that are considered ground plan features of Orthoptera, such as the saddle-shaped pronotum, the large internal cryptopleura (both representing apomorphies of Orthoptera (Wipfler *et al.* 2015)), a prothoracic pleurosternal bridge (Beier 1972), and closely associated pterothoracic pleurites that are distinctly subdivided in episternum and epimeron, whereby both substructures are almost equal in size (Beier 1972). However, Schizodactylidae also shows a number of characteristics that differ from some or all remaining ensiferan subgroups.

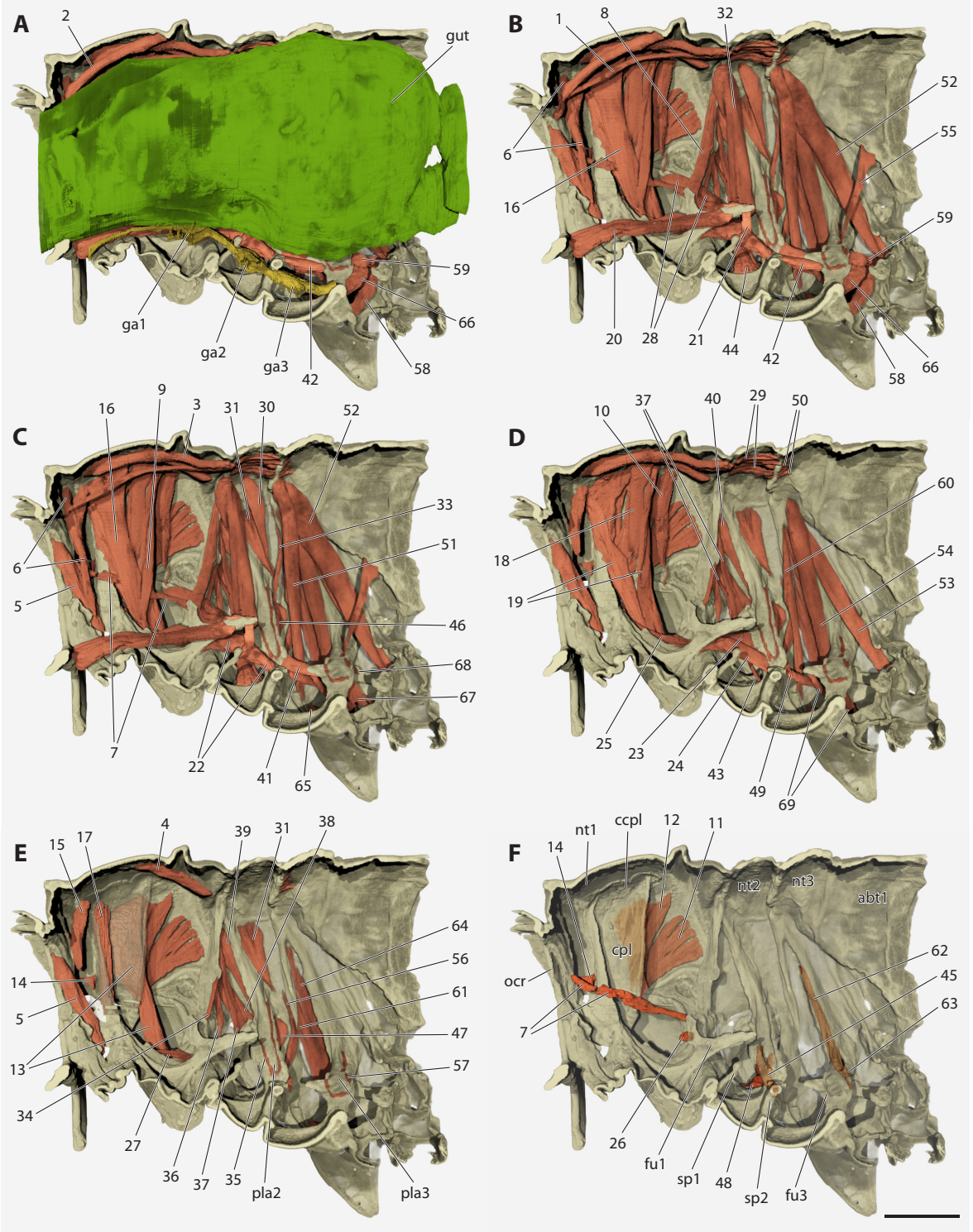


Figure 5. Thoracic muscular system of *Comicus calcaris*, three-dimensional reconstruction of right half of thorax based on SRμCT-sections. Muscles: red; skeleton: grey; digestive tract: green; nervous system: yellow. (A)–(F) Virtual dissection. Abbreviations: *abt1* 1st abdominal tergum, *cpl* cryptopleura, *ccpl* contact area of cryptopleura, *fu1/2/3* pro-/meso-/metafurca, *ga1/2/3* pro-/meso-/metathoracic ganglion, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm; *sp1/2* pro-/mesospina. For muscle terminology see text and table 1. Scale bar: 1 mm

Sternum

In particular, *Comicus* and *Schizodactylus* share some potential synapomorphies in the arrangement and characteristics of the sternal skeleton (Khattar 1960; Khattar & Srivastava 1962). In these groups, the prospinasternite (*presternite* of Khattar & Srivastava, 1962) is fused with the anterior edge of the mesosternum (Fig. 2A), thus forming a single sclerite. This situation is not found in any other studied polyneopteran, where most taxa (e.g. Grylloblattodea: Walker 1938; Mantophasmatodea: Wipfler *et al.* 2015) including the ensiferan subgroups Gryllidae (Voss 1905a), Gryllotalpidae (Carpentier 1936), Anostostomatidae (Maskell 1927; O'Brien & Field 2001), Prophalangopsidae (*Cyphoderris*) and most Tettigoniidae (Naskrecki 2000) have a free-standing prospinasternite, and is thus most likely apomorphic for Schizodactylidae. The pterothoracic sterna of Schizodactylidae are firmly connected by a diagonally oriented median sclerite (Figs. 2, 3), thus forming a large and compact pterothoracic shield or plastron (Khattar & Srivastava 1962). Although the fused meso-and metasternum in Caelifera is likewise referred to as plastron (Misra 1947; Beier 1972), it differs strongly from the situation in Schizodactylidae. In contrast to Schizodactylidae, the caeliferan metasternum is at least partly nested within the mesosternum thus forming a single sclerite (Blackith & Blackith 1966; Beier 1972). Additionally, both sterna are frequently connected to the corresponding pleura via a pleurocoxal bridge in the short-horned grasshoppers (Snodgrass 1929; Blackith & Blackith 1966; de Zolessi 1968; Beier 1972). Since a similar condition is not known from other ensiferans and polyneopterans, it is also most likely apomorphic for Schizodactylidae.

Furcae

The profurca of Schizodactylidae is bifurcated with an anterior and a well-developed posterolateral arm (Fig. 4 and Khattar 1960). Among Polyneoptera, this construction is only found in some other representatives of the Ensifera, namely the hump-winged cricket *Cyphoderris monstrosa* (Naskrecki 2000), the wetas *Anabropsis* sp. (Naskrecki 2000) and *Hemideina thoracica* (Maskell 1927), and a few members of the Tettigoniidae (Naskrecki 2000). In the remaining polyneopterans the anterior arm is either bifid near the tip and stronger than the posterior one (Mantophasmatodea and Grylloblattodea: Walker 1938, Wipfler *et al.* 2015) or the profurca is undivided (most Tettigoniidae: Naskrecki 2000; *Timema*: Kristensen 1975, Tilgner *et al.* 1999; Embioptera: Rähle 1970; Gryllidae: Voss

1905b; Gryllotalpidae: Carpentier 1921, La Greca 1938; Rhaphidophoridae: Leubner *et al.* 2016, Richards 1955; Caelifera: Snodgrass 1929, Albrecht 1953, Blackith and Blackith 1966, de Zolessi 1968; Blattodea: Matsuda 1956). In hypotheses of internal ensiferan relationships, Schizodactylidae are either placed as sister to crickets and mole crickets, the 'grylloid clade' (Gwynne 1995; Legendre *et al.* 2010; Zhou *et al.* 2017), or as relatives of the remaining ensiferans, such as katydids, hump-winged crickets, and wetas, the 'tettigonioid clade' (Desutter-Grandcolas 2003; Song *et al.* 2015; Zhou *et al.* 2017). Hence, the specific structure of the profurca in Schizodactylidae resembling that of hump-winged crickets and wetas likely supports a closer relationship of Schizodactylidae to the 'tettigonioid clade', rather than to the 'grylloid clade'.

Spinae

A further condition unique for Schizodactylidae is the T-shaped structure of the mesospina (Fig. 4 and Khattar & Srivastava 1962). In Orthoptera it generally bears a short stalk (Beier 1972). In the orthopteran subgroups the distal part of the mesospina can either be flattened, fin-shaped and oriented along the longitudinal axis (Caelifera: Albrecht 1953, Blackith and Blackith 1966, de Zolessi 1968), or bear an "irregularly formed plate" (Gryllidae: Voss 1905b), five (Rhaphidophoridae: Gurney 1935, Richards 1955, Leubner *et al.* 2016; Prophalangopsidae: Naskrecki 2000; Anostostomatidae: Naskrecki 2000) or up to six processi (Tettigoniidae: Naskrecki 2000).

Musculature

The fused prospinasternite and mesosternum and the bifurcated profurca, lead to tremendous consequences for the prothoracic musculature in *Comicus*. The ventral longitudinal Musculus prospina-mesospinalis (Ivlm8) and M. prospina-mesofurcalis (Ivlm9), both connecting the prospina with apophyses of the mesothorax, are usually present in Ensifera and most Caelifera (Supplementary table and Leubner *et al.* 2016, Wipfler *et al.* 2015). Most likely due to the rigid connection of prospinasternite and mesosternum, as well as mesosternum and metasternum, these muscles lost their function in *Comicus* and are therefore reduced. Additionally, the typical ensiferan sternocoxal muscle M. prospina-coxalis (Iscm5) that originates from the prospina is absent in *Comicus*. Instead, M. profurca-coxalis lateralis (Iscm4) that attaches to the posterior furcal arm is present. Since both

muscles share a common general direction it is likely that after the fusion of the spina, M. prospina-coxalis was functionally replaced by M. profurca-coxalis lateralis as a levator of the foreleg. Due to the lack of data about the musculature of *Schizodactylus*, we currently cannot assess whether these reductions are apomorphic for Schizodactylidae or only for *Comicus*. However, the identical skeletal morphology implies that the muscular equipment might be similar in both taxa.

Wings

All species of *Comicus* are wingless, while representatives of *Schizodactylus*, the only other genus of the Schizodactylidae, are fully winged (with the exception of the brachypterous *Schizodactylus inexpectatus*) but have limited flight capability (Khattar 1972a; Hazra & Tandon 1991; Channa *et al.* 2013). Thus the absence of wings in *Comicus* is most likely a derived feature (Irish 1986). In cave crickets and other representatives of the Ensifera, secondary winglessness is accompanied by several adaptive changes regarding their thoracic morphology (Leubner *et al.* 2016). These include secondarily undifferentiated tergites, less extensive phragmata, and the absence of wing base sclerites (Leubner *et al.* 2016), modifications which are herein shown to be also present in Schizodactylidae. In contrast to wingless species of Anostostomatidae (O'Brien & Field 2001) or Rhaphidophoridae (Richards 1955; Leubner *et al.* 2016) where the tergites of the pterothorax are saddle-shaped and clearly separated to the pleurites by membranous areas, the undifferentiated pterothoracic tergites of *Comicus* are firmly connected to the pleurites of the corresponding thorax segment (Figs. 2, 3B, D). Whereas at least a decreased set of wing-steering tergopleural muscles is retained in secondarily wingless ensiferans and phasmatodeans (Leubner *et al.* 2016), not a single flight muscle is developed in *Comicus*. This complete absence of tergopleural muscles might be explained by the rigid skeletal connection of the pterothoracic tergites and pleurites leading to non-functional muscular connections of both sclerites. This assumption is likely supported by the thoracic morphology of a wingless stick grasshopper (Caelifera: Proscopiidae), whose pterothoracic tergites and pleurites show a similar immobile connection and whose tergopleural muscles are completely reduced (de Zolessi 1968).

In summary, the thorax of Schizodactylidae is characterized by various potential apomorphic characters such as the fusion of the prospinasternite with the mesosternum, a pterothoracic shield, a t-shaped mesospina and various modifications in the musculature (the latter being unknown for *Schizodactylus*). The only thoracic character concerning the systematic placement of Schizodactylidae within Ensifera is the bifurcated profurca, which supports a closer relationship with the 'tettigonioid clade' (katydids, wetas, Jerusalem crickets and allies) thus supporting the most recent molecular data sets (Song *et al.* 2015; Zhou *et al.* 2017).

Thoracic adaptations of Schizodactylidae to their life sand dunes

The most striking thoracic modification of *Comicus* is the reduction of the wings. Wing loss is a common phenomenon in pterygote insects (Wagner & Liebherr 1992) and in Orthoptera in particular (Beier 1972; Gorochov 2001). Various reasons for its occurrence have been considered including the stability of the habitat or the energetic costs of flight in extreme environments (Wagner & Liebherr 1992; Roff 1994). We can only speculate about the reason for wing reduction in *Comicus*. It is noteworthy that the winged species of *Schizodactylus* inhabit sand dunes mainly along the shoreline and/or near the riverside (Aydin 2005; Channa *et al.* 2013), more humid environments than the completely dry desert where *Comicus* occurs (Irish 1986). For insects inhabiting dry areas, the selective advantage of foraging by flight may be compensated by the disadvantage of water loss caused by this metabolically demanding activity (Cloudsley-Thompson 1975, 1991). A character for which we have better reason to assume that it is related to water saving in a very dry environment is the size of the spiracles. The mesothoracic stigma of Schizodactylidae is not externally exposed since it is embedded in the membranous area between pro- and mesopleura and hidden behind the saddle-shaped pronotum, a situation found in most Ensifera (Beier 1972). Strauß & Lakes-Harlan (2010) provide more details about the mesothoracic stigma, its structure and connection to the tibial organ in *Comicus*. Several studies (e.g. Hoy and Robert, 1996; Strauß and Stumpner, 2015) showed that in tympanate ensiferans, such as katydids (Tettigoniidae) and crickets (Gryllidae), the mesothoracic stigma is an important part of the auditory system and typically enlarged. Schizodactylidae are atympanate ensiferans and can therefore be expected to have relatively smaller mesothoracic stigmata. However, even

compared to other atypmpanate ensiferan subgroups such as Rhaphidophoridae (Jeram *et al.* 1995), Stenopelmatidae (Strauß & Lakes-Harlan 2008b) or Gryllacrididae (Strauß & Lakes-Harlan 2008a), the mesothoracic stigma of both, *Comicus* and *Schizodactylus*, is small (Ander 1939). The metathoracic stigma is not related to hearing and clearly visible in tympanate ensiferans, such as *Gryllus* Gryllidae (Voss 1905a), *Gryllotalpa* Gryllotalpidae (Carpentier 1936), *Amblycorypha* Tettigoniidae (Kramer 1944), *Hemideina* Anostostomatidae (O'Brien & Field 2001) or *Anisoura* Anostostomatidae (Ander 1933), and atympanate ensiferans like *Troglophilus* Rhaphidophoridae (Leubner *et al.* 2016) or *Stenopelmatus* Stenopelmatidae (Strauß & Lakes-Harlan 2008b). In contrast to all these species, the respective stigma of *Comicus* is of exceedingly small size (Fig. 2C). Unfortunately, there is little information about the spiracles in *Schizodactylus*, although Ander (1939) describes at least its mesothoracic spiracle as relatively small compared to other ensiferan representatives. Small and hidden stigmata are found in many insects inhabiting arid regions and are assumed to be a typical adaptation to reduce respiratory water loss (Cloudsley-Thompson 1991). We assume that this is also the case in Schizodactylidae.

Another requirement for a life in sandy habitats is the protection of the integument against abrasion. Generally, this is achieved by pubescent sclerites and longer setae that prevent the intrusion of sand grain into vulnerable membranous articulations (Cloudsley-Thompson 1991). In *Comicus* long setae cover the anterior and posterior borders of the pronotum (Fig. 3D), a situation also found in *Schizodactylus* (Khattar 1960; Aydin & Khomutov 2008). This specific setation may protect the comparatively large membranous neck region and the articulation between the prothorax and the mesothorax against the entry of sand. Additionally the prospinasternum, mesosternum and metasternum are fused to a single ventral shield in Schizodactylidae. (see Fig. 2 and Khattar & Srivastava, 1962). In psammophilous black beetle species of the Namib desert (Coleoptera: Tenebrionidae), an enlarged metasternum is considered an adaptation for the facilitated movement in the quasi-liquid medium of their sandy environment (Koch 1961, 1963). It appears plausible that the ventral shield of Schizodactylidae has a similar function. Furthermore, *Comicus* is characterized by the fusion of the undifferentiated pterothoracic terga with the pleura of the corresponding thorax segment, in addition to closely flanking pleura of the pterothorax,

thereby giving the organism a compact and robust appearance. As shown with respect to the morphology of the pronotum, these thoracic modifications probably cause a decrease of the membranous areas between the respective sclerites and hampering sand grains from penetrating these vulnerable body regions. This assumption might be supported by a comparable robust and sparsely membranous thoracic morphology observed in the likewise psammophilous ensiferans *Cooloola* and *Stenopelmatus* (Rentz 1980, 1999).

Our findings about the schizodactylan thorax and its various adaptations towards a life in sand dunes are in line with observations of other body parts, where previous studies described similar modifications. The most striking one and the eponymic character of the group ("splay footed crickets") is the extensive armature on the legs (Fig. 1A). Their extremely modified tarsi, equipped with broad lobe-like extensions, improve the locomotion on the sandy substrate as they enable fast running or jumping and prevent the animals from sinking into the loose sand (Ramme 1931). Additionally, the tarsal broadenings and the extensive tibial spines and spurs are assumed to have at least a supporting function during burrow formation (Ramme 1931; Aydin & Khomutov 2008). The mouth parts, especially the mandibles and the maxillary laciniae are enlarged and elongated (Khattar 1958; Irish 1986; Aydin & Khomutov 2008) as they are used for digging (Khattar 1972a; Aydin & Khomutov 2008). Enlarged laciniae with a similar function are also reported from *Cooloola*, a likewise fossorial and psammophilous ensiferan (Rentz 1980, 1999). The antennae of Ensifera with burrowing behavior are often markedly shortened with a reduced number of articles, e.g. in *Gryllotalpa*, *Oryctopus* (Stenopelmatidae) and *Cooloola* (Beier 1972; Rentz 1980, 1999). In contrast, antennae of Schizodactylidae are longer than the body (Irish 1986; Channa *et al.* 2013) which is related to the special behavior of Schizodactylidae lurking at the bottom of their burrow using the long antennae to explore their surrounding (*Comicus*: Fig. 1B; *Schizodactylus*: (Khattar 1972a; Channa *et al.* 2013)). In the abdomen, the full (*Comicus*: Irish, 1986) or considerable (*Schizodactylus*: Karny, 1929; Channa et al., 2013) reduction of the primarily blade-like ensiferan ovipositor in Schizodactylidae is correlated to the burrowing behavior in sand and the subsequent deposition of the eggs in their burrows (Ramme 1931; Channa *et al.* 2013). This stands in contrast to other ensiferans, where the elongated blade-like ovipositor is used to insert eggs deeply into the soil or other substrate

(Beier 1972). In summary, every part of the body of Schizodactylidae including head, thorax, wings, abdomen and legs are modified to cope with the extreme conditions in sandy and arid habitats and thus further support the idea that Schizodactylidae represent one of the most specialized lineages of long-horned grasshoppers.

References

Albrecht, F. O. 1953. *The Anatomy of the Migratory Locust*. University of London, Athlone Press, Western Printing Services Ltd., London, 1-118 pp.

Ander, K. 1933. Über *Anisoura nicobarica* m., eine bemerkenswerte Laubheuschrecke aus der Familie Gryllacrididae (Orth. Saltatoria). *Konowia*, **12**, 217–230.

Ander, K. 1939. Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria). *Opuscula Entomologica Supplementum II*, 1–306.

Aydin, G. 2005. Distribution of the dune cricket, *Schizodactylus inexpectatus* (Orthoptera: Schizodactylidae), in the Cukurova Delta, southern Turkey. *Zoology in the Middle East*, **36**, 111–113.

Aydin, G. & Khomutov, A. 2008. The biology, nymphal stages, and life habits of the endemic sand dune cricket *Schizodactylus inexpectatus* (Werner, 1901) (Orthoptera: Schizodactylidae). *Turkish Journal of Zoology*, **32**, 427–432.

Beier, M. 1972. Saltatoria (Grillen und Heuschrecken). *In*: Helmcke, J. G., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–217.

Blackith, R. E. & Blackith, R. M. 1966. The anatomy and physiology of the morabine grasshoppers II. External anatomy and comparisons with Pyrgomorphidae, Acrididae, and Proscopiidae. *Australian Journal of Zoology*, **14**, 1035–1071.

Blackith, R. E. & Blackith, R. M. 1967. The anatomy and physiology of the morabine grasshoppers. III. Muscles, nerves, tracheae, and genitalia. *Australian Journal of Zoology*, **15**, 961–998.

Carpentier, F. 1921. Sur l'endosquelette prothoracique de *Gryllotalpa vulgaris*. *Bulletin de la Classe des Sciences, Académie Royale de Belgique*, **7**, 125–134.

Carpentier, F. 1936. Le thorax et ses appendices chez les vrais et les faux Gryllotalpides. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique. 2ème Série*, **4**, 3–86.

Channa, S. A., Sultana, R. & Wagan, M. S. 2013. Morphology and burrowing behaviour of *Schizodactylus minor* (Ander, 1938) (Grylloptera: Schizodactylidae: Orthoptera) of Pakistan. *Pakistan Journal of Zoology*, **45**, 1191–1196.

Cloudsley-Thompson, J. 1975. Adaptations of Arthropoda to arid environments. *Annual Review of Entomology*, **20**, 261–283.

Cloudsley-Thompson, J. L. 1991. Adaptations for burrowing in sand, avoidance of enemies and defence. *In*: *Ecophysiology of Desert Arthropods and Reptiles*. Springer-Verlag, Berlin, Heidelberg, 114–146.

de Zolessi, L. C. 1968. Morphologie, endosquelette et musculature d'un acridien aptère (Orthoptera: Proscopiidae). *Transactions of the Royal Entomological Society of London*, **120**, 55–113.

Desutter-Grandcolas, L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta*, **32**, 525–561.

Eades, D. C., Otte, D., Cigliano, M. M. & Braun, H. 2015. Orthoptera Species File. Version 5.0/5.0. http://orthoptera.speciesfile.org. Accessed 05 Nov 2016.

Friedrich, F. & Beutel, R. G. 2008. The thorax of *Zorotypus* (Hexapoda, Zoraptera) and a new nomenclature for the musculature of Neoptera. *Arthropod Structure & Development*, **37**, 29–54.

Friedrich, F., Matsumura, Y., Pohl, H., Bai, M., Hörnschemeyer, T. & Beutel, R. G. 2013. Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. *Entomological Science*, **17**, 1–24.

Gorochov, A. V. 2001. The higher classification, phylogeny and evolution of the superfamily Stenopelmatoidea. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 3–34.

Gurney, A. B. 1935. *The External Morphology and Phylogenetic Position of the Woodland Cave Cricket (*Ceuthophilus Brevipes *Scudder; Orthoptera; Tettigoniidæ)*. University of Massachusetts Amherst, 1-46 pp.

Gwynne, D. T. 1995. Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research*, **4**, 203–218.

Hazra, A. K. & Tandon, S. K. 1991. Ecology and behaviour of a sand burrowing insect, *Schizodactylus monstrosus* (Orthoptera: Schizodactylidae). *In*: Vereesh, G. K., Rajagopal, D. & Viraktamah, C. A. (eds) *Advances in Management and Conservation of Soil Fauna*. IBH, New Delhi, 805–809.

Heads, S. W. & Leuzinger, L. 2011. On the placement of the Cretaceous orthopteran *Brauckmannia groeningae* from Brazil, with notes on the relationships of Schizodactylidae (Orthoptera, Ensifera). *ZooKeys*, **30**, 17–30.

Hoy, R. R. & Robert, D. 1996. Tympanal hearing in insects. *Annual Review of Entomology*, **41**, 433–450.

Irish, J. 1986. The species of *Comicus* Brunner v. Wattenwyl (Orthoptera: Schizodactylidae) with a discussion of their origin. *Navorsinge van die Nasionale Museum Bloemfontein*, **5**, 253–276.

Jeram, S., Rössler, W., Cokl, A. & Kalmring, K. 1995. Structure of atympanate tibial organs in legs of the cave-living Ensifera, *Troglophilus neglectus* (Gryllacridoidea, Raphidophoridae). *Journal of Morphology*, **223**, 109–118.

Jost, M. C. & Shaw, K. L. 2006. Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution*, **38**, 510–530.

Karny, H. H. 1929. Revision der Gryllacriden des Naturhistorischen Museums in Wien einschliesslich der Collection Brunner v. Wattenwyl. 1. Hälfte. *Annalen des naturhistorischen Museums in Wien*, **43**, 35–186.

Kevan, D. K. M. 1982. Orthoptera. *In*: Parker, S. P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill, Inc., New York, 352–379.

Khattar, N. 1958. Morphology of head capsule and mouth parts of *Schizodactylus monstrosus* Don. (Orthoptera). *Journal of the Zoological Society of India*, **10**, 68–81.

Khattar, N. 1960. On the morphology of the neck and thorax of *Schizodactylus monstrosus* Don. *Journal of the Zoological Society of India*, **12**, 162–174.

Khattar, N. 1972a. A description of the adult and the nymphal stages of *Schizodactylus monstrosus* (Drury) (Orthoptera). *Journal of Natural History*, **6**, 589–600.

Khattar, N. 1972b. Anatomy of the digestive organs of *Schizodactylus monstrosus* (Drury) (Orthoptera). *Journal of Natural History*, **6**, 575–588.

Khattar, N. & Srivastava, R. P. 1962. Morphology of the pterothorax of *Schizodactylus monstrosus* Don. (Orthoptera). *Journal of the Zoological Society of India*, **14**, 93–108.

Koch, C. 1961. Some aspects of abundant life in the vegetationsless sand of the Namib desert dunes: positive psammotropism in Tenebrionid-beetles. *Scientific Papers of the Namib Desert Research Station*, **1**, 9–34.

Koch, C. 1963. The Tenebrionidae of Southern Africa, 29. Luebbertia plana gen. & spec. nov. with a dichotomic analysis of Stizopina (Opatrini). *Scientific Papers of the Namib Desert Research Station*, **18**, 1–87.

Kramer, S. 1944. The external morphology of the oblong-winged katydid, *Amblycorypha oblongifolia* (DeGEER) (Orthoptera, Tettigoniidae). *Annals of the Entomological Society of America*, **37**, 167–192.

Kristensen, N. P. 1975. The phylogeny of hexapod 'orders '. A critical review of recent accounts. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **13**, 1–44.

La Greca, M. 1938. La muscolatura di *Gryllotalpa gryllotalpa* (L.). *Archivio Zoologico Italiano*, **27**, 217–319.

Legendre, F., Robillard, T., Song, H., Whiting, M. F. & Desutter-Grandcolas, L. 2010. One hundred years of instability in ensiferan relationships. *Systematic Entomology*, **35**, 475–488.

Leubner, F., Hörnschemeyer, T. & Bradler, S. 2016. The thorax of the cave cricket *Troglophilus neglectus*: anatomical adaptations in an ancient wingless insect lineage (Orthoptera: Rhaphidophoridae). *BMC Evolutionary Biology*, **16**, 39.

Maki, T. 1938. Studies on the thoracic musculature of insects. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University*, **24**, 1–343.

Maskell, F. G. 1927. The anatomy of *Hemideina thoracica*. *Transactions of the Royal Society of New Zealand*, **57**, 637–669.

Matsuda, R. 1956. The comparative morphology of the thorax of two species of insects. *Microentomology*, **21**, 1–65.

Misra, S. D. 1947. Studies on the somatic musculature of the desert locust, *Schistocerca gregaria* (Forskal). Part III. The pterothorax. *Indian Journal of Entomology*, **9**, 19–72.

Naskrecki, P. 2000. *The Phylogeny of Katydids (Insecta: Orthoptera: Tettigoniidae) and the Evolution of Their Acoustic Behaviour.* University of Conneticut, 403 pp.

O'Brien, B. & Field, L. H. 2001. Morphology and anatomy of New Zealand wetas. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New York, 127–162.

Ragge, D. R. 1955. *The Wing-Venation of the Orthoptera Saltatoria. With Notes on Dictyopteran Wing-Venation.* British Museum (Natural History), London, 1-159 pp.

Rähle, W. 1970. Untersuchungen am Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakow 1906 (Embioptera, Embiidae). *Zoologische Jahrbücher. Abteilung Anatomie und Ontogenie der Tiere*, **87**, 248–330.

Ramme, W. 1931. Systematisches, Verbreitung und Morpho-Biologisches aus der Gryllacriden-Unterfamilie Schizodactylinae (Orth). *Zeitschrift für Morphologie und Ökologie der Tiere*, **22**, 163–172.

Rentz, D. C. F. 1980. A new family of ensiferous Orthoptera from the coastal sands of southeast Queensland. *Memoirs of the Queensland Museum*, **20**, 49–63.

Rentz, D. C. F. 1999. Pearson's Monster, a new species of *Cooloola* Rentz from Queensland (Orthoptera: Cooloolidae). *Journal of Orthoptera Research*, **8**, 25–32.

Richards, A. M. 1955. The anatomy and morphology of the cave-orthopteran *Macropathus filifer* Walker, 1869. *Transactions of the Royal Society of New Zealand*, **83**, 405–452.

Roff, D. A. 1994. The evolution of flightlessness: is history important? *Evolutionary Ecology*, **8**, 639–657.

Sharov, A. G. 1968. Phylogeny of the Orthopteroidea. *Transactions of the Institute of Paleontology. Academy of Sciences of the USSR*, **118**, 1–251.

Snodgrass, R. E. 1929. The thoracic mechanism of a grasshopper, and its antecedents. *Smithsonian Miscellaneous Collections*, **82**, 1–111.

Snodgrass, R. E. 1935. *Principles of Insect Morphology*. 1993rd ed. McGraw-Hill, Inc., New York, London, 1-667 pp.

Song, H., Am, C., Marta, M., Desutter-, L., Heads, S. W., Huang, Y., Otte, D. & Whiting, M. F. 2015. 300 million years of diversification : elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics*, **31**, 621–651.

Strauß, J. & Lakes-Harlan, R. 2008a. Neuroanatomy and physiology of the complex tibial organ of an atympanate ensiferan, *Ametrus tibialis* (Brunner von Wattenwyl, 1888)

(Gryllacrididae, Orthoptera) and evolutionary implications. *Brain, Behavior and Evolution*, **71**, 167–180.

Strauß, J. & Lakes-Harlan, R. 2008b. Neuroanatomy of the complex tibial organ of *Stenopelmatus* (Orthoptera: Ensifera: Stenopelmatidae). *The Journal of Comparative Neurology*, **511**, 81–91.

Strauß, J. & Lakes-Harlan, R. 2010. Neuroanatomy of the complex tibial organ in the splay-footed cricket *Comicus calcaris* Irish 1986 (Orthoptera: Ensifera: Schizodactylidae). *The Journal of Comparative Neurology*, **518**, 4567–4580.

Strauß, J. & Stumpner, A. 2015. Selective forces on origin, adaptation and reduction of tympanal ears in insects. *Journal of Comparative Physiology A*, **201**, 155–169.

Tilgner, E. H., Kiselyova, T. G. & McHugh, J. V. 1999. A morphological study of *Timema cristinae* Vickery with implications for the phylogenetics of Phasmida. *Deutsche Entomologische Zeitschrift*, **46**, 149–162.

Voss, F. 1905a. Über den Thorax von *Gryllus domesticus*. Erster Teil. Das Skelett. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (2)**, 268–514.

Voss, F. 1905b. Über den Thorax von *Gryllus domesticus*. Zweiter Teil. Die Muskulatur. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 355–521.

Wagner, D. L. & Liebherr, J. K. 1992. Flightlessness in insects. *Trends in Ecology & Evolution*, **7**, 216–220.

Walker, E. M. 1938. On the anatomy of *Gylloblatta campodeiformis* Walker. 3. Exoskeleton and musculature of the neck and thorax. *Annals of the Entomological Society of America*, **31**, 588–640.

Wipfler, B., Klug, R., Ge, S.-Q., Bai, M., Göbbels, J., Yang, X.-K. & Hörnschemeyer, T. 2015. The thorax of Mantophasmatodea, the morphology of flightlessness, and the evolution of the neopteran insects. *Cladistics*, **31**, 50–70.

Zeuner, F. E. 1939. *Fossil Orthoptera Ensifera*. British Museum (Natural History), London, 1-321 pp.

Zhou, Z., Zhao, L., Liu, N., Guo, H., Guan, B., Di, J. & Shi, F. 2017. Towards a higher-level Ensifera phylogeny inferred from mitogenome sequences. *Molecular Phylogenetics and Evolution*, **108**, 22–33.

Acknowledgements

We thank Susanne Neupert and René Köhler (Zoological Institute/Biocenter at University of Cologne, Germany) for providing the photograph of *Comicus* in its natural habitat and Hans Pohl (Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum at Friedrich-Schiller-University of Jena, Germany) for providing the professional photo stacks of *Comicus*. We acknowledge support by the German Research Foundation (WI 4324/1-1) and Thomas Hörnschemeyer (HO 2306/10-1).

Authors' contributions

FL, SB and BW designed the study. BW collected the material and performed the µCT-scan. FL and BW analyzed CT data. FL made the illustrations and wrote the first draft. FL, SB and BW edited drafts and contributed to writing. All authors read and approved the final manuscript.

Supplementary Table 1. Proposed homology of the thoracic musculature of *Comicus* (present study), *Conocephalus* (Maki 1938), *Acheta* (Voss 1905b), *Troglophilus* (Leubner *et al.* 2016), *Locusta* (Maki 1938), *Locusta* (Albrecht 1953), *Atractomorpha* (Maki 1938), Eumastacidae (Blackith & Blackith 1967), *Dissosteira* (Snodgrass 1929), and *Cephalocoema* (de Zolessi 1968). Peculiar characteristics regarding the thoracic musculature of *Comicus* are highlighted by color. Light blue: thoracic muscles present in *Comicus* that are lacking in Ensifera, Caelifera or both. Light green: Muscles lacking in *Comicus* that are present in Ensifera, Caelifera or both.

		ENSIFERA				CAELIFERA					
		Comicus colcaris (Schizodactylidae, wingless) (present study)	*Troglophilus neglectus* (Rhaphidophoridae, wingless) (Leubner et al, 2016)	*Conocephalus maculatus* (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* (Caelifera, winged) (Maki, 1938)	*Locusta migratoria migratoria* (Caelifera, winged) (Albrecht, 1953)	*Atractomorpha sinensis* (Caelifera, brachypterous) (Maki, 1938)	Eumastacidae (Caelifera, wingless) (Blackith & Blackith, 1967)	*Dissosteira carolina* (Caelifera, winged) (Snodgrass, 1929)	*Cephalocoema albrechti* (Caelifera, wingless) (de Zolessi, 1968)
PROTHORAX	ldlm1	1	m1	1	0dlm2	1	49	1	49	49	-
Muscle	ldlm2	2	-	5	0dlm1	5, 6	47, 48	5	47	47, 48	47, 48
homologized	ldlm3	-	m2	-	odlm1a	2	56	2	56	56	49
after Friedrich &	ldlm4	-	-	4	-	-	-	-	-	-	-
Beutel, 2008	ldlm5	3	m3	2	ldlm3a, ldlm3b	-	-	-	-	-	-
	ldlm6	4	-	3	-	3 (2 bdl), 4	58, 58a, 58b	3, 4	58	58	58, 58a
	ldvm1	?	m4	7	0dvmδ	11	52x	10	52x	-	-
	ldvm2	5	m5	9	0dvmγ	13	50	11	50	50	50
	ldvm3	-	m5	10	0dvmβ	14	51	12	51	51	51
	ldvm4	6?	-	-	0dvmα, 0dvmα'	-	-	-	52a	-	52x
	ldvm5	-	m6	11?	0ism	-	53	-	53	53	-
	ldvm6	-	-	12	0ism2	15, 16	52, 52a	13, 14	52b, 52c	52a, 52b	52, 53
	ldvm7	-	-	-	-	-	-	-	-	-	-
	ldvm8	-	-	-	-	-	-	-	-	-	-
	ldvm9	7	-	-	-	-	-	-	-	-	-
	ldvm10	8	m7	13	lism	17	59	15	59	59	59?
	ldvm11	-	-	-	-	-	-	-	-	-	-
	ldvm12	-	-	-	-	-	-	-	-	-	-
	ldvm13	9	m8	15	ldvm1 (1905), ldvm6 (1912)	20	62, 62a	17	62, 62a	62	62
	ldvm14	-	-	-	-	-	-	-	-	-	-
	ldvm15	-	-	-	-	-	-	-	-	-	-
	ldvm16	10	m9	18	ldvm2	22	63	20	63	63	65
	ldvm17	11	m9?	19	ldvm7	23	65	21	65	65	63
	ldvm18	12	m10	20	lpm6	24	64	22	64	64	64
	ldvm19	13	m11	25	ldvm8, lpm6a	30	71d	27	71d	71d	71d
	ltpm1	-	-	-	0vlm5a	-	-	-	-	-	-
	ltpm2	14, 15	-	-	0idvm1, 0idvm2	18	57	16	-	57	-
	ltpm3	-	-	-	-	-	-	-	-	-	-

Supplementary Table 1. Proposed homology of the thoracic musculature of *Comicus* (present study), *Conocephalus* (Maki 1938), *Acheta* (Voss 1905b), *Troglophilus* (Leubner *et al.* 2016), *Locusta* (Maki 1938), *Locusta* (Albrecht 1953), *Atractomorpha* (Maki 1938), Eumastacidae (Blackith & Blackith 1967), *Dissosteira* (Snodgrass 1929), and *Cephalocoema* (de Zolessi 1968). Peculiar characteristics regarding the thoracic musculature of *Comicus* are highlighted by color. Light blue: thoracic muscles present in *Comicus* that are lacking in Ensifera, Caelifera or both. Light green: Muscles lacking in *Comicus* that are present in Ensifera, Caelifera or both. *(continued)*

	ENSIFERA				CAELIFERA					
	Comicus calcaris (Schizodactylidae, wingless) (present study)	*Troglophilus neglectus* (Rhaphidophoridae, wingless) (Leubner et al, 2016)	*Conocephalus maculatus* (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* (Caelifera, winged) (Maki, 1938)	*Locusta migratoria migratoria* (Caelifera, winged) (Albrecht, 1953)	*Atractomorpha sinensis* (Caelifera, brachypterous) (Maki, 1938)	Eumastacidae (Caelifera, wingless) (Blackith & Blackith, 1967)	*Dissosteira carolina* (Caelifera, winged) (Snodgrass, 1929)	*Cephalocoema albrechti* (Caelifera, wingless) (de Zolessi, 1968)
ltpm4	-	-	-	lpm9, lpm11, lpm12	-	-	-	-	-	-
ltpm5	-	-	-	-	-	-	-	-	-	-
ltpm6	-	-	-	-	-	-	-	-	-	-
lspm1	-	-	14	lzm	19	-	(+)*	-	-	-
lspm2	-	-	34	-	-	-	-	-	-	-
lspm3	-	-	34?	-	-	-	-	-	-	-
lspm4	-	-	-	-	-	-	-	-	-	-
lspm5	-	m12?	-	-	-	-	-	-	-	-
lspm6	-	-	-	-	-	-	-	-	-	-
lspm7	-	-	-	-	-	-	-	-	-	-
lpcm1	-	-	-	-	-	-	-	-	-	-
lpcm2	-	m13	16	0vlm2	-	-	-	-	-	-
lpcm3	16	-	?	lpm5	-	-	18	-	-	-
lpcm4	17	m14	23	lpm4	28	68	26	68a, 68b	68a, 68b	68
lpcm5	18	m15	24	?	29	68a	25	68c	?	68a
lpcm6	-	-	-	-	-	-	-	-	-	-
lpcm7	-	-	-	-	-	-	-	-	-	-
lpcm8	19	m16	26, 27	lpm4a, ldvm5	31, 32	71b, 71b	28	71b, 71c, 71x	71b, 71c	71b, 71e
lvlm1	-	-	-	0vlm3	8, 9	-	7, 8	-	-	-
lvlm2	-	-	-	-	-	-	-	-	-	-
lvlm3	20	m17	6	0vlm4, 0vlm5	7	55	6	55	55	55, 55a
lvlm4	21	m18	8	lvlm7	12	61	-	61	61	-
lvlm5	-	-	-	-	-	-	-	-	-	-
lvlm6	22	m19	?	lvlm6	-	-	-	-	-	-
lvlm7	23, 24	m20	31	lvlm4, lvlm5	37	60	32	60	60	60
lvlm8	-	m21	32	lvlm1	38	88	-	88	-	88
lvlm9	-	m22	33	lvlm3	39	87	33	87	87	87
lscm1	25	m23, m24, m25	17	lbm1	21	?	19	anterior rotator of the fore coxa	-	-
lscm2	26	m26	21	lbm2	-	-	-	-	-	66

Supplementary Table 1. Proposed homology of the thoracic musculature of *Comicus* (present study), *Conocephalus* (Maki 1938), *Acheta* (Voss 1905b), *Troglophilus* (Leubner *et al.* 2016), *Locusta* (Maki 1938), *Locusta* (Albrecht 1953), *Atractomorpha* (Maki 1938), Eumastacidae (Blackith & Blackith 1967), *Dissosteira* (Snodgrass 1929), and *Cephalocoema* (de Zolessi 1968). Peculiar characteristics regarding the thoracic musculature of *Comicus* are highlighted by color. Light blue: thoracic muscles present in *Comicus* that are lacking in Ensifera, Caelifera or both. Light green: Muscles lacking in *Comicus* that are present in Ensifera, Caelifera or both. *(continued)*

		ENSIFERA				CAELIFERA					
		Comicus calcaris (Schizodactylidae, wingless) (present study)	*Troglophilus neglectus* (Rhaphidophoridae, wingless) (Leubner et al, 2016)	*Conocephalus maculatus* (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* (Caelifera, winged) (Maki, 1938)	*Locusta migratoria migratoria* (Caelifera, winged) (Albrecht, 1953)	*Atractomorpha sinensis* (Caelifera, brachypterous) (Maki, 1938)	Eumastacidae (Caelifera, wingless) (Blackith & Blackith, 1967)	*Dissosteira carolina* (Caelifera, winged) (Snodgrass, 1929)	*Cephalocoema albrechti* (Caelifera, wingless) (de Zolessi, 1968)
	Iscm3	27	m27	22	Ibm3	27	69	24	69	69	-
	Iscm4	28	-	-	-	-	66?	-	66?	66	69
	Iscm5	-	m28	-	Ibm7	25, 26	67	23	67	67	69a
	Iscm6	-	-	28?	Ibm4	-	-	29	-	-	67
	Iscm7	-	m29	43	Ivlm2	-	-	-	87x	-	-
MESOTHORAX	IIdlm1	29	m30	29	IIdlm1, IIdlm2	33	81	30	-	81	-
	IIdlm2	-	-	30	IIdlm3, IIdlm4	34, 35, 36	-	31	-	82	-
	IIdvm1	-	-	36	IIdvm7	40, 41, 42	83, 84	34, 35, 36	-	83, 84	-
	IIdvm2	-	-	41	IIdvm1, IIdvm6	51	89	41	89	89	89
	IIdvm3	-	-	-	-	58?	-	-	-	-	-
	IIdvm4	30	m31	45	IIdvm3+4	53	90	43	90	90	91
	IIdvm5	30?	m31	46	IIdvm2	54	91	44	91	91	90
	IIdvm6	31	m32	47	IIpm6	55	99	45	99	99	90a
	IIdvm7	32	m33	54	IIdvm5	62	103b, 103c	52, 53	103b, 103c	103b, 103c	103d, 103b?
	IIdvm8	33	-	-	IIism	43	-	-	F	-	F
	IIdvm9	-	-	-	-	-	-	-	-	-	-
	IItpm1	-	-	-	IIpm10	44	-	-	-	-	-
	IItpm2	-	-	37	IIpm11	45	-	-	-	-	-
	IItpm3	-	-	-	-	-	-	-	-	-	-
	IItpm4	-	-	-	-	-	-	-	-	-	-
	IItpm5	-	-	38	IIpm9	46	-	-	-	-	-
	IItpm6	-	-	-	-	-	-	-	-	-	-
	IItpm7	-	-	-	-	-	-	-	-	-	-
	IItpm8	-	-	-	IIpm13?	-	-	-	-	-	-
	IItpm9	-	-	39	IIpm12, IIpm13?	47	85	37, 38	tergopleural muscle	85	-
	IItpm10	-	m34	-	IIpm7	48	-	-	-	-	-
	IItpm11	-	-	-	-	-	-	-	-	-	-
	IItpm12	-	-	-	-	-	-	-	-	-	-
	IIItpm13	-	-	-	-	-	-	-	-	-	-
	IIppm1	34	-	-	IIpm5d+e	-	-	-	-	-	-

Supplementary Table 1. Proposed homology of the thoracic musculature of *Comicus* (present study), *Conocephalus* (Maki 1938), *Acheta* (Voss 1905b), *Troglophilus* (Leubner *et al.* 2016), *Locusta* (Maki 1938), *Locusta* (Albrecht 1953), *Atractomorpha* (Maki 1938), Eumastacidae (Blackith & Blackith 1967), *Dissosteira* (Snodgrass 1929), and *Cephalocoema* (de Zolessi 1968). Peculiar characteristics regarding the thoracic musculature of *Comicus* are highlighted by color. Light blue: thoracic muscles present in *Comicus* that are lacking in Ensifera, Caelifera or both. Light green: Muscles lacking in *Comicus* that are present in Ensifera, Caelifera or both. *(continued)*

		ENSIFERA				CAELIFERA					
		Comicus calcaris (Schizodactylidae, wingless) (present study)	*Troglophilus neglectus* (Rhaphidophoridae, wingless) (Leubner et al, 2016)	*Conocephalus maculatus* (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* (Caelifera, winged) (Maki, 1938)	*Locusta migratoria migratoria* (Caelifera, winged) (Albrecht, 1953)	*Atractomorpha sinensis* (Caelifera, brachypterous) (Maki, 1938)	Eumastacidae (Caelifera, wingless) (Blackith & Blackith, 1967)	*Dissosteira carolina* (Caelifera, winged) (Snodgrass, 1929)	*Cephalocoema albrechti* (Caelifera, wingless) (de Zolessi, 1968)
	IIppm2	-	-	-	-	-	-	-	-	-	-
	IIspm1	-	-	-	IIpm14	49	97	39	-	97	-
	IIspm2	35	m35	40	IIzm	50	86	40	86	86	86
	IIspm3	-	-	61	IIifm	-	-	-	-	-	-
	IIspm4	-	-	-	-	-	-	-	-	-	-
	IIspm5	-	-	-	-	-	-	-	-	-	-
	IIspm6	-	m36	-	-	-	-	-	-	-	-
	IIspm7	-	-	-	-	-	-	-	-	-	-
	IIspm8	-	-	-	-	-	-	-	-	-	-
	IIpcm1	36	m38	53?	IIpm5b+c	61	98	51	-	98	94
	IIpcm2	37	m39	42, 53	IIpm1, IIpm2	-	-	-	-	-	-
	IIpcm3	38	m40	51, 52	IIpm4, IIpm5a	59, 60	94, 95	49, 50	94, 95	94, 95	95
	IIpcm4	39	m40	(52)	(IIpm5a)	60	96	50	96	96	96
	IIpcm5	40	m41	55	IIpm3	-	-	-	-	-	-
	IIpcm6	-	-	-	-	-	-	-	-	-	-
	IIvlm1	-	-	35?	-	-	-	-	-	-	-
	IIvlm2	-	-	-	-	-	-	-	-	-	-
	IIvlm3	41	m42	59	IIvlm4, IIvlm5	67	116	-	-	116	-
	IIvlm4	-	-	-	-	-	-	-	-	-	-
	IIvlm5	42	m43	60	IIvlm3	68	117	-	117	117	117
	IIvlm6	-	-	-	-	-	-	-	-	-	-
	IIvlm7	-	-	-	-	-	-	-	-	-	-
	IIscm1	43, 44	m44, m45	44	IIbm1	52	92	42	92	92	92
	IIscm2	-	-	-	IIbm2	-	-	-	-	-	-
	IIscm3	45	m46	50	IIbm3, IIbm6	57	100	48	100	100	100
	IIscm4	46	m47	49?	IIbm5	56?	101	47?	101	101	101
	IIscm5	47	m48	48	IIbm7	-	93	46	93	93	93, 93a
	IIscm6	48	m49	56	IIbm4	63	103d	54	103d	103d	103c
	IIscm7	49	m50	68	IIvlm2	81	-	-	-	-	-
METATHORAX	IIIdlm1	50	m51	58	IIIdlm1	66	112	57, 58?	-	112	-

Supplementary Table 1. Proposed homology of the thoracic musculature of *Comicus* (present study), *Conocephalus* (Maki 1938), *Acheta* (Voss 1905b), *Troglophilus* (Leubner *et al.* 2016), *Locusta* (Maki 1938), *Locusta* (Albrecht 1953), *Atractomorpha* (Maki 1938), Eumastacidae (Blackith & Blackith 1967), *Dissosteira* (Snodgrass 1929), and *Cephalocoema* (de Zolessi 1968). Peculiar characteristics regarding the thoracic musculature of *Comicus* are highlighted by color. Light blue: thoracic muscles present in *Comicus* that are lacking in Ensifera, Caelifera or both. Light green: Muscles lacking in *Comicus* that are present in Ensifera, Caelifera or both. *(continued)*

	ENSIFERA				CAELIFERA					
	Comicus calcaris (Schizodactylidae, wingless) (present study)	*Troglophilus neglectus* (Rhaphidophoridae, wingless) (Leubner et al, 2016)	*Conocephalus maculatus* (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* (Caelifera, winged) (Maki, 1938)	*Locusta migratoria migratoria* (Caelifera, winged) (Albrecht, 1953)	*Atractomorpha sinensis* (Caelifera, brachypterous) (Maki, 1938)	Eumastacidae (Caelifera, wingless) (Blackith & Blackith, 1967)	*Dissosteira carolina* (Caelifera, winged) (Snodgrass, 1929)	*Cephalocoema albrechti* (Caelifera, wingless) (de Zolessi, 1968)
IIIdlm2	-	-	-	IIIdlm1a, IIIdlm3, IIIdlm4	-	-	-	-	-	-
IIIdvm1	-	-	-	-	71	113	60	-	113	-
IIIdvm2	51	m52	66	IIIdvm1, IIIdvm6	80	118	67	118	118	118
IIIdvm3	-	-	-	-	-	-	-	-	-	-
IIIdvm4	52	m53	70	IIIdvm3, IIIdvm4	84, 85	119	70	120	119	119a+b
IIIdvm5	52?	m54	71	IIIdvm2	86	120	71	119	120	119
IIIdvm6	53	m55	72	IIIpm6	87	129	72	129	129	120
IIIdvm7	54	m56	79	IIIdvm5	95, 96	133b, 133c	79, 80	133b, 133c	133b, 133c	133d, 133b?
IIIdvm8	55	-	-	IIIism	72	-	61	Fa	-	Fa
IIItpm1	-	-	-	IIIpm10, IIIpm8?	73	-	-	-	-	-
IIItpm2	-	-	62	IIIpm11	74	-	-	tergopleural inter-segmental muscle?	-	-
IIItpm3	-	-	-	-	-	-	-	-	-	-
IIItpm4	-	-	-	-	-	-	-	-	-	-
IIItpm5	-	-	-	IIIpm9	75	-	-	-	-	-
IIItpm6	-	-	-	-	-	-	-	-	-	-
IIItpm7	-	-	-	-	-	-	-	-	-	-
IIItpm8	-	-	-	-	-	-	-	-	-	-
IIItpm9	-	-	63	IIIpm12	76	114	62, 63	tergopleural muscle	114	-
IIItpm10	-	m57	64	IIIpm7	-	-	-	-	-	-
IIItpm11	-	-	-	-	-	-	-	-	-	-
IIItpm12	-	-	-	-	-	-	-	-	-	-
IIItpm13	-	-	-	-	-	-	-	-	-	-
IIIppm1	56	-	-	-	-	-	-	-	-	-
IIIppm2	-	-	-	-	-	-	-	-	-	-
IIIspm1	-	-	-	-	77, 78	127	64, 65	-	127	-
IIIspm2	57	m58	65	IIIzm	79	115	66	115	115	115

Supplementary Table 1. Proposed homology of the thoracic musculature of *Comicus* (present study), *Conocephalus* (Maki 1938), *Acheta* (Voss 1905b), *Troglophilus* (Leubner *et al.* 2016), *Locusta* (Maki 1938), *Locusta* (Albrecht 1953), *Atractomorpha* (Maki 1938), Eumastacidae (Blackith & Blackith 1967), *Dissosteira* (Snodgrass 1929), and *Cephalocoema* (de Zolessi 1968). Peculiar characteristics regarding the thoracic musculature of *Comicus* are highlighted by color. Light blue: thoracic muscles present in *Comicus* that are lacking in Ensifera, Caelifera or both. Light green: Muscles lacking in *Comicus* that are present in Ensifera, Caelifera or both. *(continued)*

	ENSIFERA				CAELIFERA					
	Comicus calcaris (Schizodactylidae, wingless) (present study)	*Troglophilus neglectus* (Rhaphidophoridae, wingless) (Leubner et al, 2016)	*Conocephalus maculatus* (Tettigoniidae, winged) (Maki, 1938)	*Acheta domesticus* (Gryllidae, winged) (Voss 1905, 1912)	*Locusta migratoria migratorioides* (Caelifera, winged) (Maki, 1938)	*Locusta migratoria migratoria* (Caelifera, winged) (Albrecht, 1953)	*Atractomorpha sinensis* (Caelifera, brachypterous) (Maki, 1938)	Eumastacidae (Caelifera, wingless) (Blackith & Blackith, 1967)	*Dissosteira carolina* (Caelifera, winged) (Snodgrass, 1929)	*Cephalocoema albrechti* (Caelifera, wingless) (de Zolessi, 1968)
IIIspm3	-	-	-	-	-	-	-	-	-	-
IIIspm4	-	-	-	-	-	-	-	-	-	-
IIIspm5	59, 58?	m59?	-	-	-	-	-	-	-	-
IIIpcm1	60	m60	78?	IIIpm5b	78	128	94	-	128	125
IIIpcm2	61	m61	67, 78	IIIpm1, IIIpm2	-	-	-	-	-	-
IIIpcm3	62	m62	76, 77	IIIpm4	76, 77	125	92, 93	125	125	125a
IIIpcm4	63	m62	(77)	IIIpm5a	77	126	93	126	126	126
IIIpcm5	64	m63	80	IIIpm3	-	-	-	-	-	-
IIIpcm6	-	-	-	-	-	-	-	-	-	-
IIIpcm7	-	-	-	-	-	-	-	-	-	-
IIIvlm1	-	-	-	-	70	-	59	A, B	-	-
IIIvlm2	-	-	88	IIIvlm2-5	104	144	87	144	?	144?
IIIvlm3	-	-	85	IIIvlm1	103	143	86	143	?	143?
IIIscm1	65	m64	69	IIIbm1	82, 83	121 (pair)	68, 69	121	121	121, 121a
IIIscm2	66	m65	73	IIIbm2	88	123, 124	73	123, 124	123, 124	123, 124
IIIscm3	67	m66	75	IIIbm3	90, 91	130	75	130	130	130
IIIscm4	68	m67	74	IIIbm5	89	122	74	122	122	130a
IIIscm5	-	-	-	-	-	-	-	-	-	-
IIIscm6	69	m68	81	IIIbm4	97	133d	81	133d	133d	133c

CHAPTER 3

Phylogeny of the Orthoptera based on morphology, with focus on Ensifera, bioacoustics and the significance of wing-associated stuctures

Fanny Leubner & Sven Bradler

Abstract

The Orthoptera, or Saltatoria, represents an exceedingly diverse insect group among the lower neopterans, or Polyneoptera, well known for the widespread capability of acoustic communication. In particular, members of its subgroup Ensifera, the long-horned grasshoppers (crickets, katydids and allies), have been extensively studied in regard of aspects of sound production and processing. Nevertheless, the phylogenetic placement of orthopterans among Polyneoptera as well as its internal relationships has been controversially discussed in the past, and different phylogenetic schemes in numerous studies emphasize their unstable phylogenetic affinities. Especially a deeper understanding of an evolutionary scenario related to bioacoustics for Ensifera is currently hindered due to the lack of a stable phylogenetic backbone. Based on a phylogenetic analysis of morpho-anatomical characters of the thorax, the present study provides a novel hypothesis of the systematic placement of Orthoptera among Neoptera, and the internal relationships of Ensifera. In congruence with preceding phylogenetic hypotheses, the presented phylogeny supports a close relationship of Orthoptera to a group comprising earwigs (Dermaptera), stick insects (Phasmatodea), roaches and mantids (Dictyoptera), heel walkers (Mantophasmatodea), and ice crawlers (Grylloblattodea). Xenonomia (Mantophasmatodea + Grylloblattodea) are found to form the sister taxon to Orthoptera, which is supported by a pronotum that is laterally connected to the propleura, the absence of Musculus mesofurca-coxalis posterior (IIscm2), and the secondary absence of M. metanoto-trochantinalis posterior (IIIdvm3). The internal relationships among Ensifera are well resolved, and a subdivision in two major clades, the ‘grylloid’ and the ‘tettigonioid clade’ is supported. In contrast to previous phylogenetic hypotheses, the ‘tettigonioid clade’ is composed of Tettigoniidae (katydids and bush-crickets) as sister to all the remaining tettigonioid lineages: raspy crickets (Gryllacrididae), dune crickets (Schizodactylidae), cave crickets (Rhaphidophoridae), hump-winged crickets (Prophalangopsidae), Jerusalem crickets (Stenopelmatidae), and king crickets (Anostostomatidae). With regard to an evolutionary scenario of bioacoustics, this phylogenetic scheme supports the current view of multiple convergent origins of tegminal stridulation within the Ensifera. This form of intraspecific communication evolved at least in three lineages: the ‘grylloid clade’, in Tettigoniidae, and in Prophalangopsidae.

Introduction

Studying the morphology, neurobiology, behaviour and ecology of grasshoppers, crickets, katydids and their allies has always been the subject of numerous research efforts. With more than 27 500 extant species, Orthoptera (or Saltatoria) forms one of the most speciose taxa among the lower neopteran insect lineages (Grimaldi & Engel 2005; Eades *et al.* 2015). Besides the polar regions, they are widespread across all continents and show an overwhelming abundance in diversity and inhabit all terrestrial habitats (Beier 1972; Kevan 1982). Orthoptera is subdivided into two major lineages: Caelifera (short-horned grasshoppers: locusts, grasshoppers and allies) and Ensifera (long-horned grasshoppers: crickets, katydids, wetas and allies). Morphological characters such as the large saddle-shaped pronotum, an internal cryptopleura and the saltatorial hind legs exhibiting a straightened femur-tibia articulation in combination with a conceivable reduction of the trochanter strongly support monophyly of Orthoptera (Kristensen 1991; Grimaldi & Engel 2005; Kluge 2016).

Systematic placement of Orthoptera among Neoptera

The Neoptera, insects that can fold their wings over the abdomen, are traditionally subdivided in three main groups: Holometabola (characterized by a pupal stage and complete metamorphosis), Paraneoptera (characterized by sucking mouth parts), and a group termed 'Lower Neoptera' or Polyneoptera. Whereas monophyly of Holometabola is not questioned (e.g. Beutel *et al.* 2011; Misof *et al.* 2014), that of Paraneoptera and Polyneoptera has been frequently challenged (reviewed in Trautwein *et al.* 2012; Yeates *et al.* 2012). Only within recent years, phylogenetic studies agree on a monophyletic Polyneoptera (e.g. Ishiwata *et al.* 2011; Letsch & Simon 2013; Misof *et al.* 2014; Wipfler *et al.* 2015; Song *et al.* 2016). Probably due to their ancient rapid radiation, the relationships among the major polyneopteran lineages in particular are poorly understood (Whitfield & Kjer 2008). Including heel walkers (Mantophasmatodea), a polyneopteran taxon as recently discovered as 2002 (Klass *et al.* 2002), the Polyneoptera comprises praying mantises or mantids (Mantodea), roaches and termites (Blattodea), earwigs (Dermaptera), stick and leaf insects (Phasmatodea), webspinners (Embioptera), stoneflies (Plecoptera), angel insects (Zoraptera), ice crawlers (Grylloblattodea), and grasshoppers and relatives

(Orthoptera). Among Polyneoptera, several monophyletic entities were repeatedly proposed in phylogenetic studies. These include among others the taxa Dictyoptera, comprising Mantodea and Blattodea (including termites) (Fig. 1), Xenonomia, a group comprising Mantophasmatodea and Grylloblattodea (e.g. Terry & Whiting 2005; Misof *et al.* 2014), and and Eukinolabia, containing Phasmatodea and Embioptera (e.g. Friedemann *et al.* 2012; Misof *et al.* 2014).

Besides a few phylogenetic studies based on 18S and 28S rDNA, in which Orthoptera was found as sister to Holometabola (Yoshizawa & Johnson 2005; Wang *et al.* 2013),

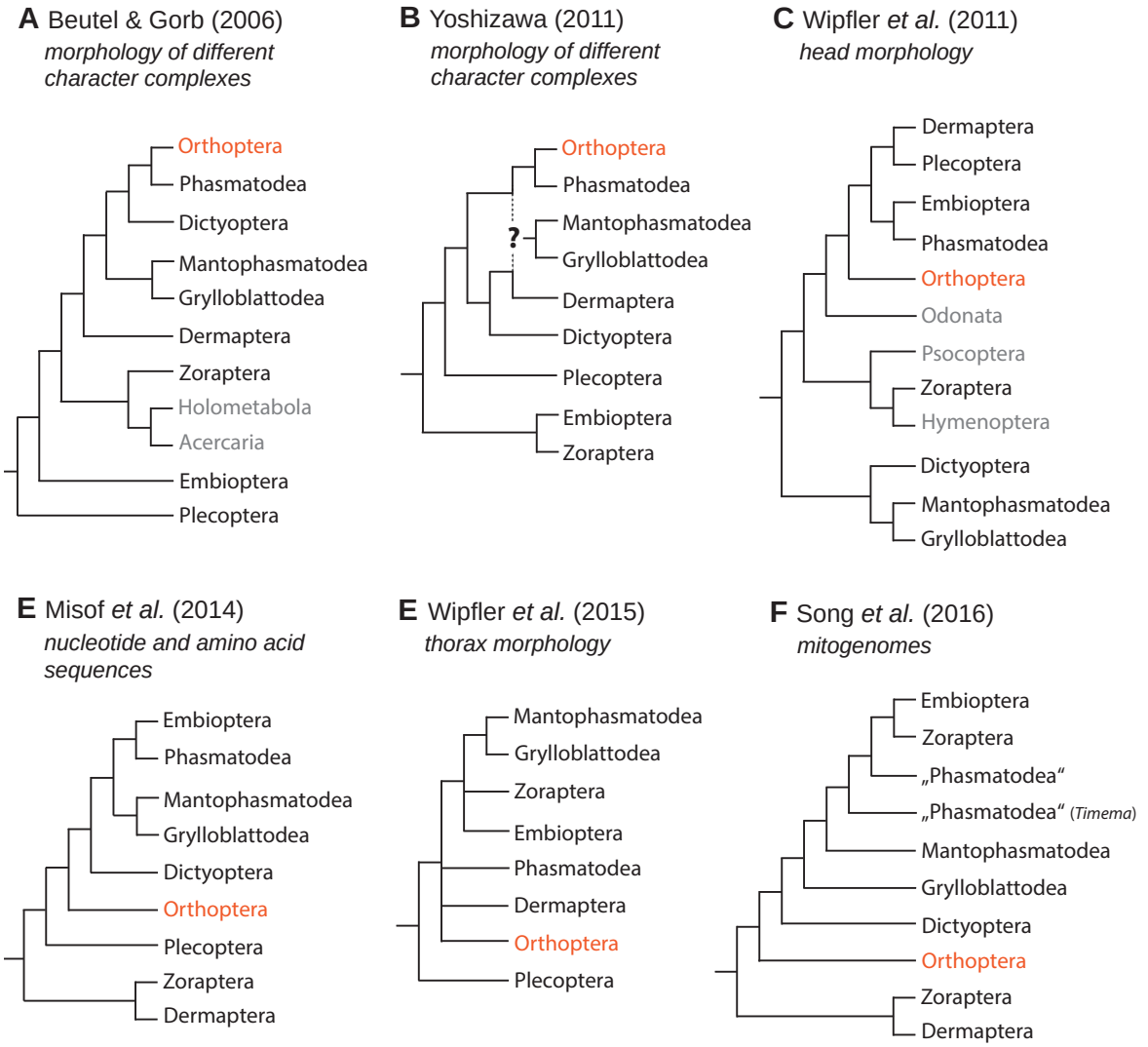


Figure 1. Systematic placement of Orthoptera. Presented phylogenetic hypotheses include representatives of all polyneopteran lineages, especially members of Mantophasmatodea and Grylloblattodea. Hypotheses in A and C proclaim paraphyletic Polyneoptera.

the phylogenetic affinity of Orthoptera to Polyneoptera was repeatedly confirmed in both morphological and molecular phylogenies (Fig. 1). Nevertheless, the phylogenetic placement of Orthoptera among Polyneoptera is unstable across data sets and analyses and widely varies in published phylogenies (Fig. 1). Recent cladistic studies that include all aforementioned distinguished polyneopteran lineages either propose a closer relationship of Orthoptera to Phasmatodea (Fig. 1A: Beutel & Gorb 2006, Fig. 1B: Yoshizawa 2011), Eukinolabia (Terry & Whiting 2005), or to Dictyoptera + Zoraptera (Ishiwata *et al.* 2011; Sasaki *et al.* 2013). Nevertheless, numerous phylogenetic studies suggest Orthoptera to form the sister group to clades comprising a number of other polyneopteran lineages. These potential sister clades either comprise Eukinolabia, Dermaptera, and Plecoptera (Fig. 1C: Wipfler *et al.* 2011), Xenonomia, Eukinolabia, and Dictyoptera (Fig. 1E: Misof *et al.* 2014), or Mantophasmatodea, Grylloblattodea, Embioptera, Zoraptera, Phasmatodea, and Dictyoptera (Fig. 1F: Song *et al.* 2016). Especially phylogenies based on different morphological character systems (Fig. 1A–D) emphasize the unstable phylogenetic placement of Orthoptera. With respect to present cladistic analyses of morphological characters, the aforementioned problems make it impossible to choose a single most suitable outgroup taxon for studies focusing on Orthoptera and call for the inclusion of representatives of all major polyneopteran lineages.

Internal relationships of long-horned grasshoppers (Ensifera)

Orthoptera in general have long been of interest to scientists studying acoustic communication and hearing systems (Robinson & Hall 2002). Especially the acoustic signalling and sound processing of crickets (Gryllidae) and bush-crickets or katydids (Tettigoniidae) are popular research topics that gain widespread interest among scientists (e.g. Gwynne 2001; Korsunovskaya 2008; Strauß *et al.* 2014a). Nevertheless, a deeper understanding of the evolution of bioacoustics for Ensifera is currently hindered due to the lack of a stable backbone phylogeny. Traditional classifications of Ensifera are based on informal analyses of different morphological character systems (Fig. 2). These taxonomic hypotheses show major disagreement upon higher relationships, even in those based on the same morphological character system (see Fig. 2B–D). The extraordinary work of Ander (1939) was the first to combine different morphological character systems for

a vast number of ensiferan taxa. In light of recent phylogenetic studies, Ander's work is surprisingly modern and truly ahead of its time, as his phylogenetic conclusions were exclusively based on shared-derived characters and, in addition, was published roughly ten years before Hennig (1950) formulated his fundamentals in phylogenetic systematics. Ander (1939) assumed the Ensifera to be divided into two major lineages: crickets, mole crickets and relatives (Grylloidea therein) and a separated lineage comprising cave crickets (Rhaphidophoridae), dune crickets (Schizodactylidae), raspy crickets (Gryllacrididae), Jerusalem crickets, king crickets and wetas (his 'Stenopelmatidae' include the members of the Anostostomatidae), hump-winged crickets (Prophalangopsidae), and katydids

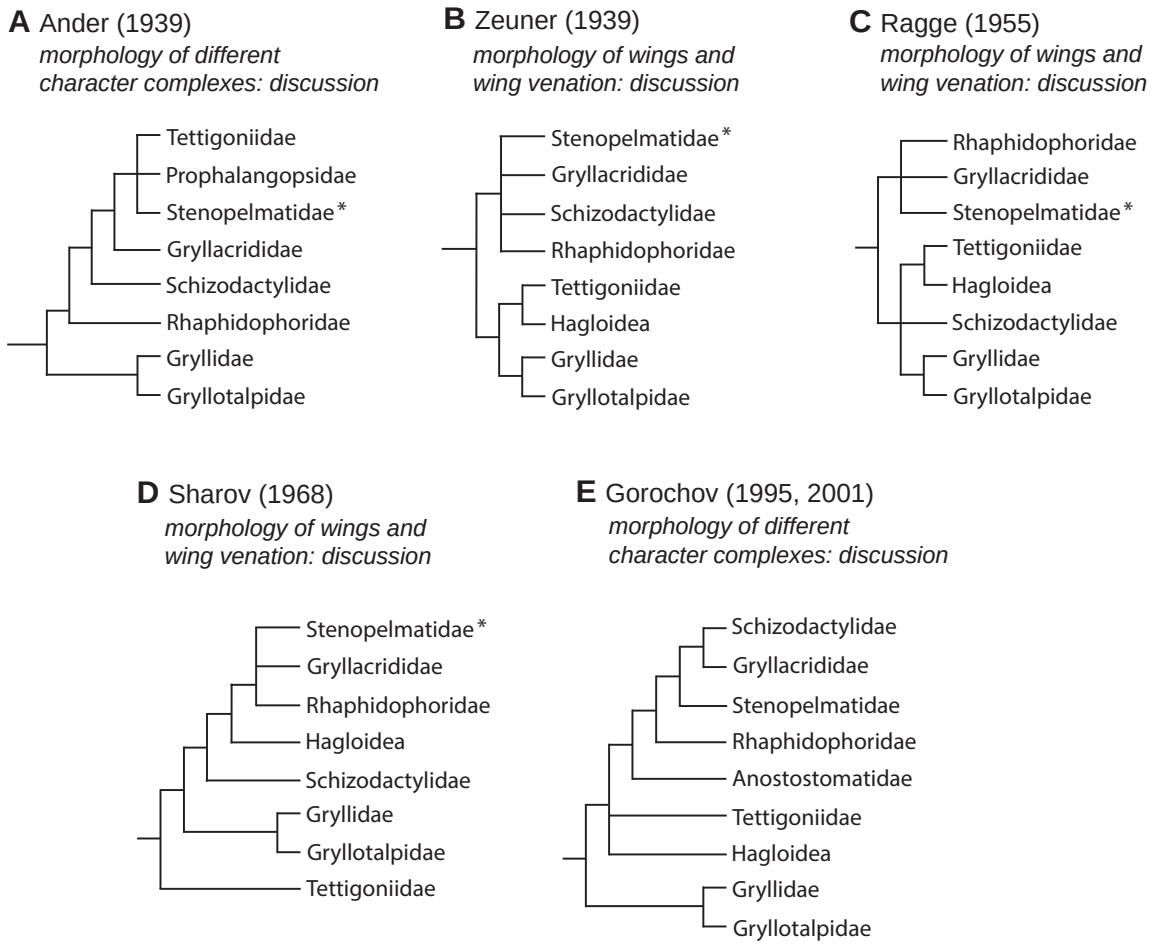


Figure 2. Hypotheses of ensiferan relationships based on the discussion of morphological characters after different authors. The taxon Stenopelmatidae in (A)-(D) includes the taxon Anostostomatidae (marked by asterisk *). Following the classification scheme of Eades *et al.* (2015), the term Hagloidea aggregates extinct and fossil representatives of that ensiferan lineage. The term Hagloidea is therefore only used, when the author additionally studied fossil representatives of that taxon. The term Prophalangopsidae is used, when the author only studied the extant genera of the Hagloidea.

(Tettigoniidae) (Fig. 2A). This major split of Ensifera in a 'grylloid clade' and a 'tettigonioid clade' gained further evidence in subsequent informal analyses (Fig. 2E: Gorochov 1995b, 2001), formal cladistic analyses of morphological characters (Fig. 3), and analyses of molecular data (Fig. 4). With studies available based on morphology, mitochondrial genomes, sequences of various single genes, or ribosomal DNA, the previous proposed phylogenetic relationships of Ensifera using formal cladistic analyses are now based on a wide spectrum of character systems. Nevertheless, almost every imaginable variant towards the internal relationships of the 'tettigonioid clade' and its affiliation of dune crickets (Schizodactylidae) was proposed in at least partly drastically different phylogenetic hypotheses (Fig. 2–4). This instability of ensiferan relationships was most recently highlighted by Zhou *et al.* (2017), who received two completely different phylogenetic schemes by analyzing the same mitochondrial genome data with two differing models (compare Fig. 4C and D).

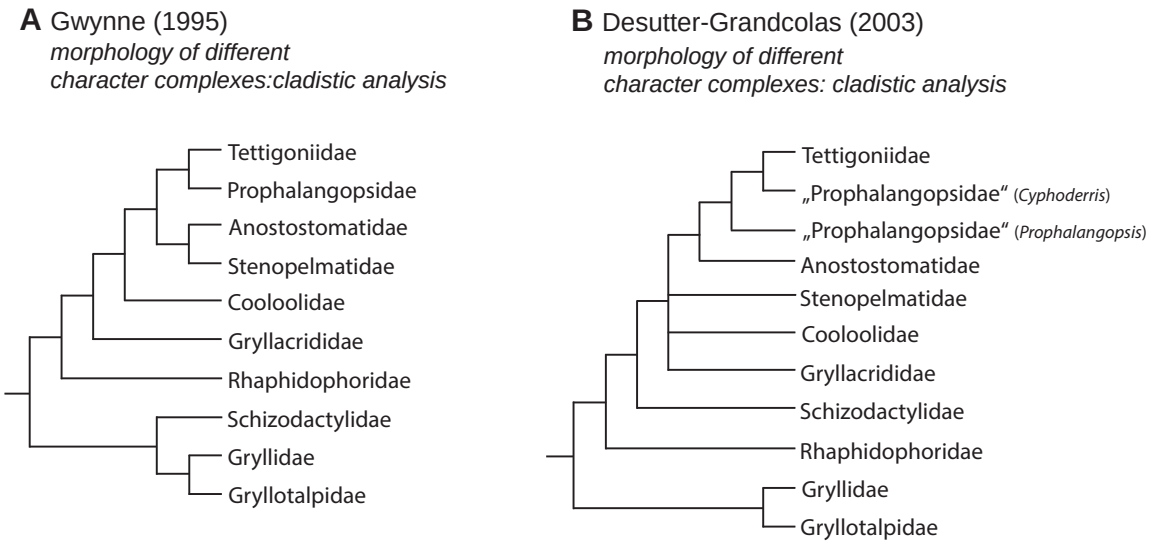


Figure 3. Hypotheses of ensiferan relationships based on a formal cladistic analysis of morphological characters after different authors. Since no fossil representatives of the Hagloidea were studied by the authors the term Prophalangopsidae is used following the classification scheme of Eades *et al.* (2015).

Regarding the 'tettigonioid clade', cave-crickets (Rhaphidophoridae) were frequently assumed to form a basal lineage diverging from the remaining tettigonioids (Fig. 2A: Ander 1939, Fig. 3A: Gwynne 1995 (Gwynne places Schizodactylidae as sister to the 'grylloid clade'), Fig. 3B: Desutter-Grandcolas 2003). Legendre *et al.* (2010) re-evaluated the phylogenetic analysis of 18S, 28S and 16S rRNA sequences previously conducted by

Jost and Shaw (Jost & Shaw 2006) and even found Rhaphidophoridae to form the sister to all remaining ensiferans (Fig. 4A).

Until now, the hypothesis of a basal position of the non-singing and deaf cave crickets in phylogenetic frameworks was in congruence with studies of their hearing organs, which appear to have a primarily primitive structure showing no signs of an ancestral capability of hearing (Stritih & Stumpner 2009; Stritih & Čokl 2012; Strauß *et al.* 2014b). This theory must now be reconsidered in the light of recent novel phylogenetic hypotheses, in which

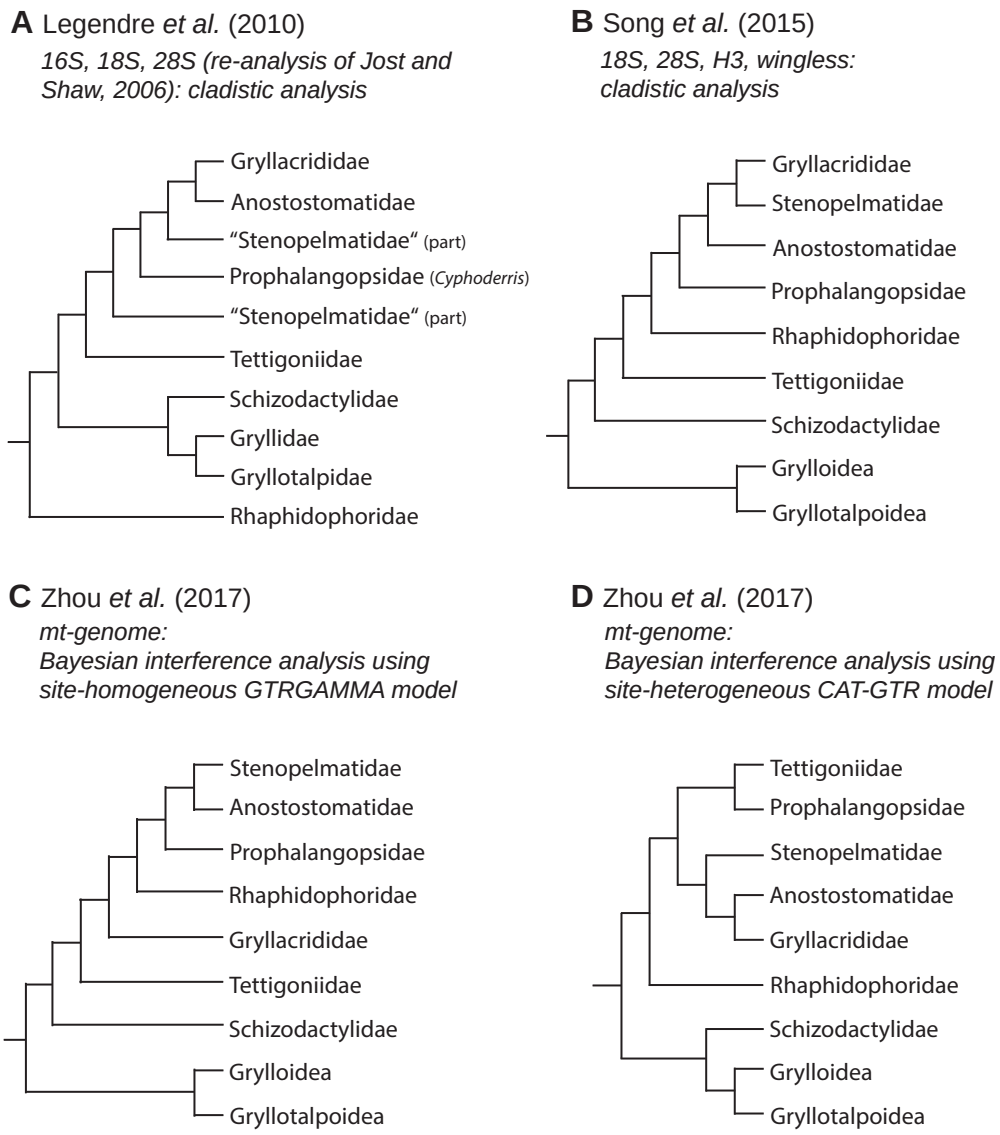


Figure 4. Hypotheses of ensiferan relationships based on cladistic analyses of molecular data after different authors. Since no fossil representatives of the Hagloidea were studied by the authors the term Prophalangopsidae is used following the classification scheme of Eades *et al.* (2015).

cave crickets are assumed to be more closely related to king and Jerusalem crickets, and to the singing hump-winged crickets (Fig. 4B: Song *et al.* 2015, Fig. 4C: Zhou *et al.* 2017). On the other hand, hump-winged crickets (Prophalangopsidae) were traditionally placed as the sister taxon to katydids (Tettigoniidae), since members of both families are capable of communicating by tegminal stridulation and perceiving sounds by a functional tympanal organ (Fig. 2B–D). Therefore, formal cladistic analyses including these morphological characters confirmed a monophyletic origin of both taxa (Fig. 3). In contrast to the opinion of a single evolutionary origin of tegminal stridulation in Ensifera (Alexander 1962; Otte 1992), these phylogenetic schemes support an independent origin of tegminal stridulation in at least two lineages: in crickets + mole crickets and in hump-winged crickets + katydids (Gwynne 1995; Desutter-Grandcolas 2003). To the contrary, recent phylogenetic studies based on molecular data reject a sister relationship of Prophalangopsidae and Tettigoniidae, and instead propose a closer relationship of Prophalangopsidae to Jerusalem crickets (Stenopelmatidae), king crickets (Anostostomatidae) and/or raspy crickets (Gryllacrididae) (Fig. 4A–C). Unfortunately, both of these studies drew no concrete conclusions on the resulting consequences for the evolution of bioacoustics within Ensifera, but indicate even more origins of tegminal stridulation in Ensifera than previously assumed. In this regard, a critical reanalysis of this character system is crucial to present a well-founded evolutionary scenario of ensiferan bioacoustics. In addition, generating more data of phylogenetic significance is necessary to evaluate all these former contradicting hypotheses.

The main objective of the present study lies in the examination and documentation of a yet neglected morphological character system in ensiferans. Based on a comprehensive taxon sampling covering major caeliferan and ensiferan lineages, the morphological groundpattern of the orthopteran thorax regarding its skeleton and musculature is reconstructed. Characters of the skeletal and muscular system of the thorax that were used in a previous cladistic analysis of major neopteran lineages (Wipfler *et al.* 2015) are re-evaluated and complemented by novel orthopteran-specific characters. These characters are combined for a formal cladistic analysis to illuminate the phylogenetic affinities and systematic placement of Orthoptera among Neoptera, and to propose a novel phylogenetic hypothesis of internal ensiferan relationships. Additionally, the evolution of bioacoustics within the Ensifera is thoroughly reviewed and discussed on the basis of the new results.

Material and methods

Taxon sampling

In total, 39 terminal taxa were sampled. For a list of the studied taxa, see Table 1. The sample of the ingroup taxon represents 23 taxa covering the phylogenetic diversity of Orthoptera as currently recognized (Song *et al.* 2015). Specifically, extant representatives of all major ensiferan lineages, crickets (Gryllidae), mole crickets (Gryllotalpidae), katydids (Tettigoniidae), raspy crickets (Gryllacrididae), dune crickets (Schizodactylidae), Jerusalem crickets (Stenopelmatidae), cave crickets (Rhaphidophoridae), hump-winged crickets (Prophalangopsidae), and king crickets (Anostostomatidae) were included. Naming of the orthopteran species as well as their taxonomical affiliation follows the current classification of Eades *et al.* (2015). Since the phylogenetic affinities of Orthoptera within the Polyneoptera, and also the most "basal" taxon within Polyneoptera are still unknown (e.g. Yoshizawa 2011; Letsch and Simon 2013; Misof et al. 2014; Song et al. 2016), the outgroup is represented by at least one representative of each polyneopteran subgroup, in addition to certain representatives of the Paraneoptera, Holometabola, and the palaeopteran taxon Ephemeroptera. The outgroup selection depends on a previous approach based on 119 morphological characters of the thorax (Wipfler *et al.* 2015). For convenience, only the generic names of the investigated taxa are used in the following.

Table 1. List of examined species including information on taxonomy, distribution (collection site), µCT scan, sex and (additional) literature used for coding characters.

						(additional) literature	
taxon		**species**	**distribution (collection site)**	**CT-scan**	**sex**	**skeleton**	**musculature**
Caelifera	Tridactylidae Brullé, 1835	*Xya* sp Latreille, 1809	Eurasia, Africa, Southeast Asia, Australia (Germany)	SRµCT BESSY Berlin, 11/2011	♀	Carpentier 1936	Carpentier 1936
	Eumastacoidea Burr, 1899 Morabinae Rehn, 1948	-	-	-	?	Blackith & Blackith 1966, 1969	Blackith & Blackith 1967
	Proscopiidae Serville, 1838	*Cephalocoema albrechti* (de Zolessi, 1968)	Uruguay, Argentinia	-	?	de Zolessi 1968	de Zolessi 1968
	Acrididae McLeay, 1821	*Dissosteira carolina* (Linnaeus, 1758)	Northern America, Southeastern U.S.A.	-	?	Snodgrass 1929	Snodgrass 1929

Table 1. List of examined species including information on taxonomy, distribution (collection site), µCT scan, sex and (additional) literature used for coding characters. *(continued)*

						(additional) literature	
taxon		**species**	**distribution (collection site)**	**CT-scan**	**sex**	**skeleton**	**musculature**
	Acrididae McLeay, 1821	*Locusta migratoria* (Linnaeus, 1758)	Europe, Southern Africa, Southeast Asia	-	?	Albrecht 1953	Albrecht 1953
	Acrididae McLeay, 1821	*Schistocerca gregaria* (Forskål, 1775)	Northern Africa	-	?	Misra 1946, 1947	Misra 1946, 1947
	Acrididae McLeay, 1821	*Stenobothrus lineatus* (Panzer, 1796)	Middle Europe (Germany)	µCT Kiel, 08/2014	♀	-	-
Ensifera	Gryllidae Laicharting, 1781	*Acheta domesticus* (Linnaeus, 1758)	Europe	-	?	Voss 1905a,b	Voss 1905c, 1912
	Gryllidae Laicharting, 1781	*Gryllus bimaculatus* De Geer, 1773	Southern Europe, Northern Africa (breeding in Germany)	SRµCT DESY Hamburg, 2012	♀	-	-
	Gryllotalpidae Leach, 1815	*Gryllotalpa gryllotalpa* (Linnaeus, 1758)	Europe	µCT Greifswald, 02/2014	?	Carpentier 1921, 1936; La Greca 1938	La Greca 1938
	Rhaphidophoridae Walker, 1869	*Troglophilus* (*Paratroglophilus*) *neglectus* Krauss, 1879	Southeastern Europe (Slowenia)	SRµCT BESSY Berlin, 2011	♀		
	Gryllacrididae Blanchard, 1845	*Prosopogryllacris* sp Karny, 1937	Southeast Asia, Phillipines, Japan, Papua New Guinea	SRµCT DESY Hamburg, 07/2014	♀	-	-
	Stenopelmatidae Burmeister, 1838	*Stenopelmatus* sp Burmeister, 1838	Western North America	SRµCT DESY Hamburg, 07/2014	♀	-	-
	Anostostomatidae Saussure, 1859	*Papuaistus* sp Griffini, 1911	Asia-Tropical (Papua New Guinea)	µCT Kiel, 08/2014	♀	-	-
	Anostostomatidae Saussure, 1859	*Hemideina crassidens* (Blanchard, 1851)	Southeastern Australia, New Zealand (New Zealand)	µCT Kiel, 08/2014	♀	Maskell 1927; O'Brien & Field 2001	-
	Prophalangopsidae Kirby, 1906	*Cyphoderris monstrosa* Uhler, 1864	Northern America (Northwestern U.S.A.)	SRµCT DESY Hamburg, 07/2014	♂	Naskrecki 2000	-
	Schizodactylidae Blanchard, 1845	*Comicus calcaris* Irish, 1986	Southern Africa (Namibia)	SRµCT DESY Hamburg, 2012	♀	Irish 1986	-
	Schizodactylidae Blanchard, 1845	*Schizodactylus monstrosus* (Drury, 1770)	Asia-Tropical, Indian Subcontinent, Bengal	-	?	Khattar 1960, 1972; Khattar & Srivastava 1962	-
	Tettigoniidae Krauss, 1902	*Tettigonia viridissima* (Linnaeus, 1758)	Europe (Germany)	µCT Kiel, 08/2014	♀	Naskrecki 2000	-
	Tettigoniidae Krauss, 1902	*Conocephalus* (*Anisoptera*) *dorsalis* (Latreille, 1804)	Southwestern Europe (Germany)	µCT Greifswald, 02/2014	♀	Naskrecki 2000	Maki 1938
	Tettigoniidae Krauss, 1902	*Pholidoptera griseoaptera* (De Geer, 1773)	Northern Europe (Germany)	µCT Kiel, 08/2014	♀	Naskrecki 2000	-

Table 1. List of examined species including information on taxonomy, distribution (collection site), µCT scan, sex and (additional) literature used for coding characters. *(continued)*

						(additional) literature	
taxon		**species**	**distribution (collection site)**	**CT-scan**	**sex**	**skeleton**	**musculature**
	Tettigoniidae Krauss, 1902	*Meconema meridionale* Costa, 1860	Southeastern Europe (Germany)	µCT Kiel, 08/2014	♀	Naskrecki 2000	-
	Tettigoniidae Krauss, 1902	*Meconema thalassinum* (De Geer, 1773)	Middle Europe (Germany)	µCT Greifswald, 02/2014	♀	Naskrecki 2000	-
Phasmatodea		*Megacrania tsudai* Shiraki, 1932	Taiwan	-	?	Maki 1935; Klug 2008; Bradler 2009	Maki 1935
		Timema nevadense Strohecker, 1966	Western U.S.A	-	?	Tilgner *et al.* 1999; Tilgner 2002; Klug 2008	Klug 2008
Embioptera		*Embia surcoufi* Navas, 1933	Eastern Africa, Mozambique	-	?	Rähle 1970; Barlet 1985b,c	Rähle 1970; Barlet 1985a; Klug 2008
Zoraptera		*Zorotypus hubbardi* Caudell, 1916	North America, U.S.A.	-	?	Friedrich & Beutel 2008	Friedrich & Beutel 2008
Dermaptera		*Euborellia annulipes* (Lucas, 1847)	North America, South America, Europe, India, China	-	?	Bharadwaj & Chadwick 1974b	Bharadwaj & Chadwick 1974a
Mantodea		*Stagmomantis carolina* (Johansson, 1763)	North America, Central America, Southern South America	-	?	Levereault 1938; Wieland 2006, 2013	Levereault 1938
Blattodea		*Periplaneta americana* (Linnaeus, 1758)	Southern North America, Middle Europe, Asia	-	?	Carbonell 1947; Ryuichi Matsuda 1956	Carbonell 1947
Mantophasma-todea		*Austrophasma caledonensis* Klass et al, 2003	Western South Africa, South Africa	-	?	Wipfler *et al.* 2015	Wipfler *et al.* 2015
Grylloblattodea		*Grylloblatta campodeiformis* Walker, 1914	North America	-	?	Walker 1938	Walker 1938
Plecoptera		*Perla abdominalis* Burmeister, 1839	Middle Europe, Southern Europe	-	?	Wittig 1955	Wittig 1955
Psocoptera		*Stenopsocus stigmaticus* (Imhoff & Labram, 1842)	Middle Europe	-	?	Badonell 1934	Badonell 1934
Thysanoptera		Phloeothrips coriaceus Haliday, 1836	Northern Europe, California	-	?	Mickoleit 1979	Mickoleit 1979
Neuroptera		*Palpares libelluloides* (Linnaeus, 1764)	Southern Europe	-	?	Czihak 1954	Czihak 1954
Hymenoptera		*Macroxyela ferruginea* (Say, 1824)	Northern America, U.S.A.	-	?	Vilhelmsen 2000; Vilhelmsen *et al.* 2010	Vilhelmsen 2000; Vilhelmsen *et al.* 2010
Archostemata		*Tetraphalerus bruchi* Heller, 1913	Argentina	-	?	Friedrich *et al.* 2009	Friedrich *et al.* 2009
Ephemeroptera		*Siphlonurus columbianus* McDunnough, 1925	North America, Northern U.S.A., Canada	-	?	Matsuda 1956	Matsuda 1956

Examination of specimens, micro-computed tomography (µCT) and 3D-reconstruction

The ingroup taxa that were investigated by µCT in the present study were female adults, with the exception of *Cyphoderris* (Prophalangopsidae), for which only an adult male was available (Table 1). Where appropriate, the 70%-ethanol fixed specimens were stored in alcoholic Bouin's fixative or stained in an iodine solution over night to gain more contrast of soft tissues and muscles during the computed tomography (Metscher 2009). Samples were dehydrated in a graded ethanol series, critical- point dried (Balzer CPD 030) and mounted on a specimen holder (aluminium stub). The scans were either performed at synchrotron radiation facilities or at µCT X-ray tomographs (details given in Table 1). The three-dimensional models of the thoraces were created using AMIRA® (version 5.4.3 and 6.0.0.) and the skeletomuscular system was analysed based on virtual sections. Images taken in AMIRA® were thereafter edited to adjust contrast, brightness and colour using Adobe Photoshop® CS3. Figures, plates and schematic drawings were arranged in Adobe Illustrator® CS4.

Terminology and character selection

The terminology of the thoracic skeleton largely follows Snodgrass (1935). The thoracic musculature of all examined specimens is homologized after the terminology of Friedrich & Beutel (2008). This approach is based on morphological data of the thorax concerning three different character complexes: skeleton, musculature and wing base. The skeleton complex comprises 47 characters in total. Of those, 26 characters were previously used for a cladistic analysis by Wipfler *et al.* (2015), 4 characters were modified from Wipfler *et al.* (2015), and 17 novel characters were coded. The musculature complex comprises 55 characters in total, of which 24 were used in Wipfler *et al.* (2015). The homologization of thoracic muscles by Wipfler *et al.* (2015) concerning the outgroup taxa of the present study was thoroughly reviewed and revised (see Supplementary Table 1). The third character complex, traits of the wing and wing base in particular, comprises 39 characters that combine data of the study of Beutel & Gorb (2001) and Yoshizawa (2011). Again, all of these characters were previously used in the cladistic analysis performed by Wipfler *et al.* (2015). The majority of entries into the data matrix for the skeleton and musculature are

based on observations of a single specimen for each species representing supraspecific terminal taxa (Table 1). In a few cases, additional information on the morphology of the skeleton was taken from previous studies containing more general descriptions of the genus or family (e.g. Carpentier 1936; Maki 1938; Matsuda 1970) (see Table 1). Entries for the musculature of terminal, supraspecific taxa were based on the present investigation or literature data of a single species. Only in the genus *Embia*, the thoracic musculature is a chimera combining two different species, since one study only described the prothoracic and another the pterothoracic musculature (Rähle 1970; Barlet 1985a).

Character coding and phylogenetic analyses

A cladistic analysis was performed using two datasets. The first dataset comprises 141 characters and is composed of all three character complexes, skeleton, musculature, and wing and wing base characters, which is hereafter termed 'complete dataset'. The second analysis is based on a dataset of 102 characters, in which the characters of the wing and wing base were excluded, hereafter termed 'reduced dataset'. Characters were either coded as neomorphic (binary: absent/present) or transformational ("unordered multistate") characters following Sereno (2007). All characters were equally weighted and unordered. The character state "0" is not necessarily corresponding to the assumed plesiomorphic condition. The full character matrices of both analyses are presented in a text file in the appendix (Supplementary File 1 and 2). Parsimony analyses were carried out with TNT in a traditional search (Goloboff *et al.* 2008) under different conditions: Wagner trees with 5000 (10000, 20000) random seeds, 500 (1000, 2000) replies; the swapping algorithm was set as TBR (tree bisection reconnection). Trees were rooted with the palaeopteran *Siphlonurus* (Ephemeroptera) in accordance with recent molecular-based phylogenies (Letsch & Simon 2013; Misof *et al.* 2014). Bremer support (Bremer 1994) for each node was calculated with TNT.

Results

Characters

Characters of the thoracic skeleton

1 Lateral cervical sclerites: (0) absent; (1) single pair of sclerites present; (2) two pairs of sclerites present (character 1 of Wipfler *et al.* 2015)

Within the Orthoptera, the sclerites embedded in the lateral area of the neck membrane appear in two different states. The Caelifera are characterized by two lateral cervical sclerites that are distinctly separated from each other, whereby the two sclerites are almost equal in size (e.g. Snodgrass 1929; Misra 1946; Blackith & Blackith 1966; de Zolessi 1968). In most Ensifera, the sclerotization within the neck membrane appears as a single, large lateral cervical sclerite, named lateral cervical plate by other authors (Weber 1933; Wieland 2006). Only in the dune crickets *Comicus* (Leubner *et al.* 2017) and *Schizodactylus* (Khattar 1960), two distinctly separated lateral cervical sclerites of almost equal size are present.

According to Alicata (1962), an additional rather small sclerite (Alicata's first cervical sclerite *C1*) forms the anterior articulation of the lateral cervical sclerites with the occipital rim in all representatives of the Orthoptera (except *Tetrix*) he examined. However, such a small anterior sclerite is only described by other authors in the proscopiid *Cephalocoema* (de Zolessi 1968) and the cricket *Acheta* (Voss 1905a). Matsuda (1970) reflects Alicata's opinion, and assumes that the sclerite in question is a detached part of the occipital condylus. However, the sclerite serves as an insertion point for at least two muscles: Idvm1 (*M. cervico-occipitalis anterior*) (Voss 1905a, c; Alicata 1962; de Zolessi 1968) and Idvm4 (*M. pronoto-cervicalis lateralis*) (Alicata 1962). Both muscles are proposed to be inserted on the anterior part of the first cervical sclerite (Friedrich & Beutel 2008). In contrast to the opinion of Matsuda (1970), these findings are more consistent with the assumption that the small cervical sclerite in some Orthoptera is a detached anterior part of the first (or single) cervical sclerite.

Whereas the absence of cervical sclerites is found to be an apomorphy of Coleoptera, vestiges of cervical sclerites are present in the archeostematan *Tetraphalerus* (Friedrich *et al.* 2009). These vestiges, completely merged with the proventrite, are unpaired (Friedrich *et al.* 2009).

2 Cervical sclerites and pleura: (0) separated; (1) partly or completely fused (character 2 of Wipfler *et al.* 2015)

In the majority of studied taxa, the cervical sclerites are distinctly separated from the prothoracic pleura (Matsuda 1970). Instead, the cervical sclerites of Hymenoptera are partly or completely fused with the propleura (Beutel *et al.* 2011). Also in *Palpares* (Neuroptera) at least the posterior cervical sclerite is fused with the pleura (Czihak 1954). Character coding adopted from Wipfler *et al.* (2015).

3 Dorsal cervical sclerites: (0) absent; (1) present (character 3 of Wipfler *et al.* 2015)

Within the Caelifera, dorsal cervical sclerites are frequently present in the grasshoppers *Dissosteira* (Snodgrass 1929), *Schistocerca* (Misra 1946), and *Stenobothrus*, the proscopiid *Cephalocoema* (de Zolessi 1968), and Eumastacidae (Blackith & Blackith 1967). Albrecht (1953) does not give a detailed description of the sclerites within the neck membrane, the character is therefore coded as "?". In *Xya* no dorsal cervical sclerite was observed, nor is it described for other Tridactylidae (Carpentier 1936; Alicata 1962). For Ensifera, a dorsal cervical sclerite is only described in Gryllidae (Voss 1905a) and Rhaphidophoridae (Alicata 1962; Leubner *et al.* 2016).

4 Pronotum: (0) not saddle like; (1) saddle like, cryptopleura (character 4 of Wipfler *et al.* 2015)

A saddle-shaped pronotum in combination with a cryptopleura is considered an apomorphic trait of Orthoptera (Kristensen 1991; Desutter-Grandcolas 2003; Beutel & Gorb 2006; Wipfler *et al.* 2015). A saddle-shaped pronotum is also described for a few further insect taxa, such as Zoraptera (Friedrich & Beutel 2008) or Archostemata (Friedrich *et al.* 2009). Although the pronotum is elongated in both aforementioned taxa, nearly all parts of the prothoracic pleura are not hidden by the pronotum. In contrast, the pronotum of Orthoptera is characterized by elongated lateral lobes that cover the largest part of the prothoracic pleura (see Fig. 5; after Ander 1939).

Due to the enormous dimensions of the orthopteran cryptopleura, Ander (1939) is of the opinion that this structure cannot merely be formed by the elongation of the pronotal lateral lobes, but rather through a vertical growth of the pleura itself. Thereby, the membranous border between the pronotum and propleura has been stretched

and forms the outer layer of the pleural sac (*Pleuralsack* by Ander), a structure opened at the bottom that has been formed by the invagination of the propleura (see Fig. 5). The interior part of the pleura (cryptopleura) is well-developed in all orthopterans, although the free part that can be seen from an exterior view might be reduced in great parts (Ander 1939). This idea of Ander is supported by the specific course of a muscle bundle of Idvm19 (*M. pronototrochanteralis*) that, within Ensifera, is only present in Gryllidae (*Gryllus*: see Fig. 16B at page 159; *Acheta*: Voss, 1905c). Here, the muscle Idvm19 has two bundles, the anterior one running between the cryptopleura and the pronotum. Due to this specific course the muscle bundle is rather restricted in its functionality in Gryllidae, and resulted in the reduction of this muscle bundle in other orthopteran taxa (Ander 1939).

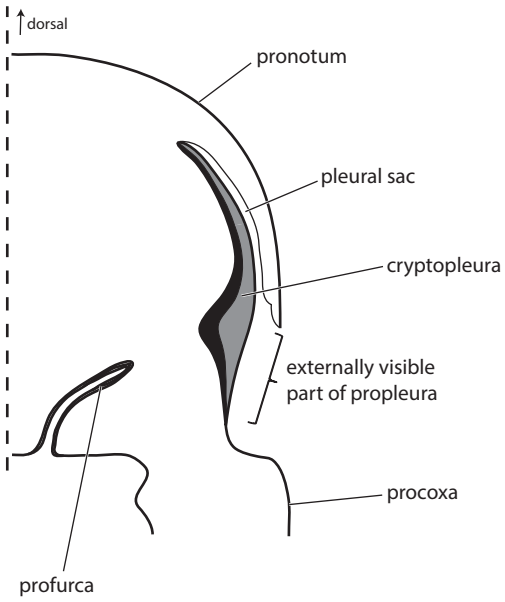


Figure 5. Schematic cross section trough prothorax of Orthoptera. The internally lying cryptopleura consists of an epithelial duplication and an externally visible part. (redrawn after Ander 1939)

5 Lateral connection of pronotum and propleura: (0) absent; (1) partly or completely connected (character 5 of Wipfler *et al.* 2015)

In Orthoptera, the pronotum and cryptopleura are closely associated. Although the pronotum might show a freestanding, overlapping edge, internal elements of the pronotum merge with at least parts of the pleura in all Orthoptera (Ander 1939). Character coding for the other studied taxa is adopted from Wipfler *et al.* (2015).

6 Prothoracic defense glands: (0) absent; (1) present (character 6 of Wipfler *et al.* 2015)

Prothoracic defense glands only occur in Phasmatodea (Bradler 2009b). Character coding adopted from Wipfler *et al.* (2015).

7 Opening of prothoracic defense glands: (0) anterior margin of pronotum; (1) below the anterior corners of pronotum (character 7 of Wipfler *et al.* 2015)

This character is only applicable to Phasmatodea. Whilst the opening of the prothoracic defense gland in *Timema* is situated near the anterior margin of the pronotum, it is positioned below the anterior pronotal corners in all other phasmatodeans (Bradler 2009). Character coding adopted from Wipfler *et al.* (2015).

8 Prothoracic anapleural ridge: (0) present; (1) absent (character 8 of Wipfler *et al.* 2015)

In Orthoptera, the prothoracic pleura appears as an internally exposed cryptopleura (see also explanation of character 4). As this skeletal element underwent numerous modifications (Ander 1939) thus impeding clear interpretations of this character, it is coded as "?" for all members of the Orthoptera, following the approach of Wipfler *et al.* (2015). Character coding for the remaining taxa is adopted from Wipfler *et al.* (2015).

9 Prothoracic anapleural invagination or wing: (0) absent; (1) present (character 9 of Wipfler *et al.* 2015)

An anapleural invagination or wing is only present in Mantophasmatodea (Wipfler *et al.* 2015) and Grylloblattodea (Walker 1938). The anapleural wing is an internal episternal apodeme that unites with the pleural ridge (Wipfler *et al.* 2015) Character coding for the remaining taxa is adopted from Wipfler *et al.* (2015).

10 Connection of propleura and prosternum: (0) precoxal bridge; (1) pleurosternal bridge; (2) precoxale; (3) membranous

The region of the pleura extending ventrally from the episternum anterior to the coxa and the trochantin is frequently sclerotized (Snodgrass 1935). Snodgrass distinguishes between two manifestations: First, the precoxal bridge that extends ventrally from the episternum and is frequently united with the sternum of the corresponding thoracic segment. Second, the precoxale that forms a distinct sclerite separated from both the episternum and the sternum (Fig. 6A). Other terms for the sclerite anterior to the coxa and trochantin are preepisternum (e.g. Friedrich & Beutel 2008; Koeth *et al.* 2012) or preepisternite (Wieland 2002, 2006), although both terms did not differentiate between the two definitions of Snodgrass (1935).

After Snodgrass (1935), the precoxal bridge is not necessarily united with the corresponding sternum, thereby summarizing two quite different character states in one term. Therefore, it is useful to establish two differing terms. Herein, the precoxal bridge of Snodgrass (1935) is defined as the ventrally extended episternum, whereby the precoxal bridge might be delimited by the episternum via a suture, but must clearly be separated from the sternum by a membranous area (Fig. 6B). The complete fusion of the pleural episternum with the sternum of the corresponding segment via a sclerotized bridge is herein referred to as pleurosternal bridge (psb; see Fig. 6C).

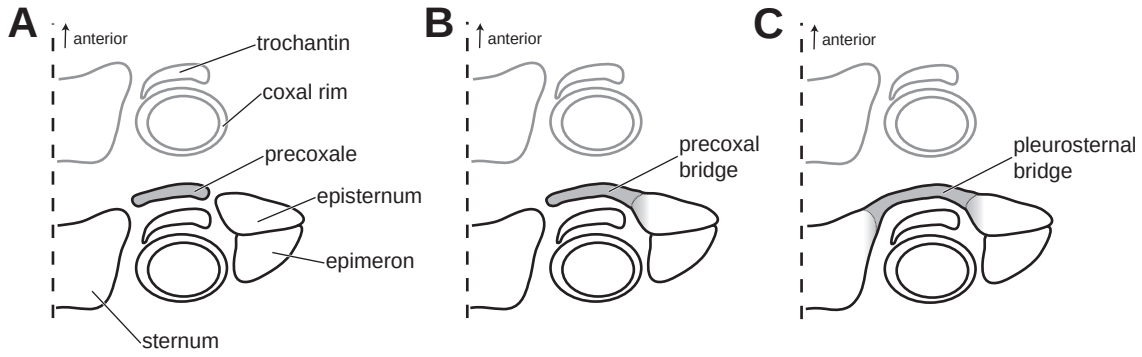


Figure 6. Precoxal connection of pleura and sternum. (A) Precoxale. Freestanding sclerite anterior to the trochantin of the respective segment. (B) Precoxal bridge. The episternum is ventrally extended, but a membranous area is situated between precoxal bridge and sternum. (C) Pleurosternal bridge. Pleura and sternum of a segment are connected via a sclerotized arch anterior to the trochantin of the respective segment.

Within the Polyneoptera, a distinct precoxale is reported from Dermaptera (Günther & Herter 1974). The anterior propleural sclerite described for Zoraptera appears as a free sclerite that articulates anteriorly with the second lateral cervical sclerite (Friedrich & Beutel 2008). Some authors refer to the anterior propleural sclerite as the precoxale (Crampton 1926; Weidner 1970b). To the contrary, Friedrich & Beutel (2008) assume the anterior propleural sclerite to be the result of fusioning the anterior part of the anepisternum with the precoxale. Nevertheless, the anterior propleural sclerite is completely separated from both, the pleura and the sternum and herein coded as character state “2”.

In Mantophasmatodea (Wipfler *et al.* 2015) and Grylloblattodea (Walker 1938), the sternal area of the prothorax is mainly membranous. The anterior corner of the prothoracic episternum forms an articulation point with the second lateral cervical sclerite. However, the prothoracic sternum does not extend ventrally to form a pleurocoxal bridge, nor is it delimited by a precoxale.

A precoxal bridge is present in Blattodea incl. Isoptera (Weidner 1970a; Beier 1974) , and is likewise reported from some representatives of the Embioptera (Matsuda 1970), although it might be entirely reduced in other embiids (Matsuda 1970; Rähle 1970). Snodgrass (1935) describes the prothorax of Plecoptera retaining in the “apterygote condition” in which the anapleurite and coxopleurite form distinct sclerites. The precoxal part of the coxopleurite gives rise to a partly or entirely free sclerite, the trochantin (Snodgrass 1935). The part of the anapleurite located anterior to the pleural ridge is homologous to the episternum of the pleuron of the remaining pterygote insects (Snodgrass 1935). The anapleurite in the prothorax of Plecoptera frequently shows an anterioventral extension (Wittig 1955; Matsuda 1970) that Matsuda interprets as the preepisternum. Following the definition herein, the described situation in Plecoptera would likely be homologous to the presence of a prothoracic precoxal bridge. Also in Phasmatodea, the anterior part of the prothoracic pleura, either as anapleurite (e.g. in *Timema*: Tilgner *et al.* 1999) or episternum (Matsuda 1970; Tilgner *et al.* 1999; Tilgner 2002) bears an anterioventral extension, that is comparable to the situation found in Plecoptera.

Within the Polyneoptera, a definite prothoracic pleurosternal bridge is only present in Orthoptera (e.g. Voss 1905a; Kramer 1944; Misra 1946; de Zolessi 1968) and Mantodea (Wieland 2002, 2013). In both taxa, the formation of the pleurosternal bridge ensures a stabilization of the prothorax. In Mantodea, the pleurosternal bridge in addition to other characters, like the lateral fusion of the furcasternites with the pronotal edge (Beier 1968a), provide the required stability of the prothorax in association with the characteristic mantodean feeding behavior.

In Orthoptera, the pleurosternal bridge is likely a stabilizing factor for the large interior cryptopleura. The cryptopleura serves as an insertion point for the extensive prothoracic musculature, mainly pleurocoxal musculature (see Supplementary Plates 3, 13, 21, 26, 36, 42, 45), and is therefore exposed to high mechanical stress. Hence, the pleurosternal

bridge in Orthoptera is a connecting element between the cryptopleura and the ventral sternite, solidly fixing the cryptopleura in its position.

In *Siphlonurus* (Ephemeroptera) the basisternum extends anterolaterally almost to the ventral edge of the anepisternum, although both structures are clearly separated by a membranous area (Matsuda 1956a). Following the given definition, in which a precoxal bridge is defined as an extension of the episternum, the character is here coded as "3". In *Stenopsocus* (Psocoptera) (Badonell 1934) and *Palpares* (Neuroptera) (Czihak 1954) a precoxal bridge is present. In Thysanoptera, the area between the prothoracic pleura and sternum is mainly membranous, the only sclerite lying in the respective area is the trochantin (Mickoleit 1979). In Hymenoptera, the propleura is completely fused with the lateral cervical sclerite and the prosternum, forming the so called propectus (Vilhelmsen 2000; Vilhelmsen *et al.* 2010). A homology to neither of the given character states is sure, the character is thereof coded as "?": In Coleoptera, all exposed body parts are strongly sclerotized (Beutel & Leschen 2005). In general, the thoracic sclerites of Coleoptera are frequently firmly connected and no membranes are exposed externally (Friedrich *et al.* 2009). In *Tetraphalerus* (Archostemata) the ventral margin of the propleural sclerite anterad of the pleurocoxal joint is firmly connected with the lateral edge of the proventrite (prosternum) and a distinct anapleural cleft is present (Friedrich *et al.* 2009). However, this situation is not comparable to the pleurosternal bridge present in Orthoptera or Mantodea. Since the homology is uncertain, the character is coded as "?" for *Tetraphalerus*.

11 Prothoracic furcasternite: (0) fused with basisternite; (1) developed as a freestanding unpaired sclerite; (2) as a freestanding, paired sclerite; (3) not distinct, just two separated spots (furcal pits) posterior to the basisternite

The majority of Orthoptera is characterized by a prothoracic sternum consisting of the fused basisternite and furcasternite (Beier 1972). This condition is also found in Zoraptera (Friedrich & Beutel 2008), Mantophasmatodea (Wipfler *et al.* 2015), Embioptera (Matsuda 1970; Rähle 1970), Dermaptera (Matsuda 1970; Günther & Herter 1974), Plecoptera (Matsuda 1970), Mantodea (Beier 1968a; Wieland 2013), and Blattodea (excl. Isoptera) (Matsuda 1956b; Storch 1968; Beier 1974). The prothorax of Phasmatodea is characterized by two clearly separated sclerotized plates (Beier 1968b). There are different opinions about the origin of these sclerites, mainly due to lacking prothoracic

furcae in Euphasmatodea (Bradler 2009). Here, the anterior sclerite is most likely a product of the fusion of the prothoracic basisternite and furcasternite, as it bears a sclerotized ridge (sternacosta?) at its posterior edge (Jeziorski 1918; Beier 1968b). This is supported by the equivalent morphology in *Timema*, the only representative of Phasmatodea with a fully developed profurca (Tilgner *et al.* 1999). The posterior plate in the prothorax of Phasmatodea is either regarded as the spinasternite (Jeziorski 1918), furcasternite (Beier 1968b), or the fused furcasternite (partly), spinasternite and mesothoracic presternum (Matsuda 1970). Since the posterior sternal plate in Phasmatodea bears the spina (Jeziorski 1918; Tilgner *et al.* 1999), the opinion of Jeziorski is followed herein and the character is coded as state "0" for Phasmatodea. The prothoracic sternal region of Grylloblattodea is mainly membranous. A sclerotized basisternite is present, a distinct furcasternite is lacking. The invagination points of the prothoracic furcae appear as two sclerotized spots posterior to the basisternite (Walker 1938). As there is no distinctly developed furcasternite, the situation in Grylloblattodea is not comparable to that found in other Polyneoptera. Hence, the character is likely an apomorphic trait of Grylloblattodea and herein coded as an isolated character state. Within the Orthoptera, only the members of Gryllidae (true crickets) are characterized by

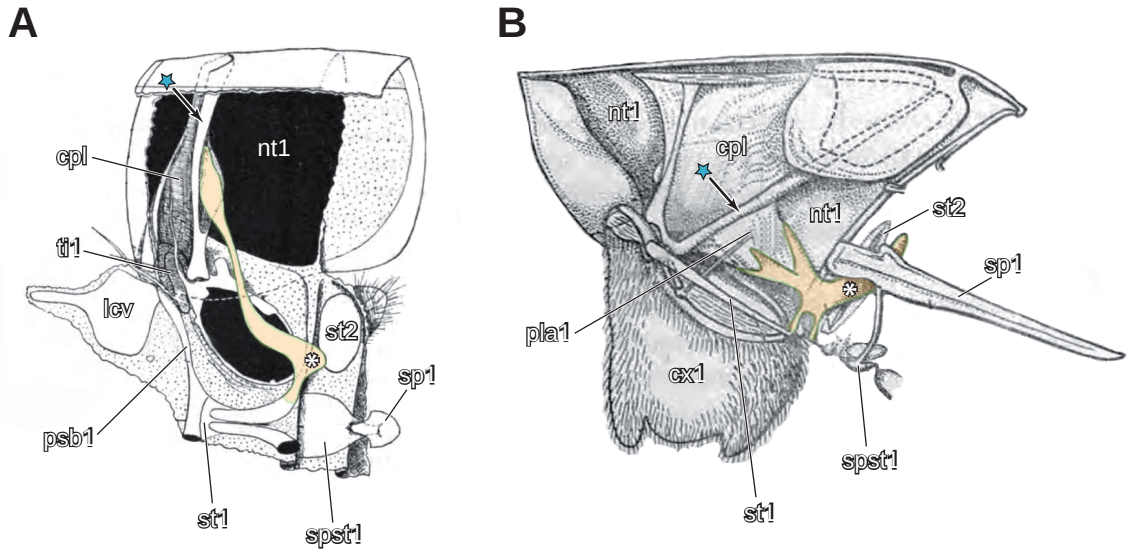


Figure 7. Morphology of the prothorax in Grylloidea. (A) *Acheta domesticus* (modified after Voss 1905a) and (B) *Gryllotalpa gryllotalpa* (modified after Carpentier 1921b). Profurca is highlighted in transparent orange. The white asterisk * marks the posterior arm-like or bulbous extension of the profurca. Blue asterisks mark the pleural ridge of cryptopleura.

a furcasternite that is distinctly separated from the basisternite via a membranous area (Beier 1972). Additionally, the furcasternite in Gryllidae shows a distinct membranous gap dividing the sclerite in two equally sized substructures (Fig. 7, Supplementary Plate 10), a situation not reported from other Ensifera and polyneopteran taxa.
In *Siphlonurus* (Ephemeroptera) (Matsuda 1956a), *Stenopsocus* (Psocoptera) (Badonell 1934), *Palpares* (Neuroptera) (Czihak 1954), and *Macroxyela* (Hymenoptera) (Vilhelmsen 2000; Vilhelmsen *et al.* 2010) the basisternite and furcasternite are indistinguishably fused. In Thysanoptera, the basisternite (*Sternum* of Mickoleit 1979) and furcasternite (*Eusternum* of Mickoleit 1979) are distinctly separated, although the basisternite is entirely reduced in some species (Mickoleit 1979). In the vast majority of Thysanoptera, the separated furcasternite forms a single sclerite (Mickoleit 1979). The single prosternal sclerite in *Tetraphalerus* (termed proventrite in Friedrich *et al.* (2009) is strongly sclerotized and consists of the fused basisternum and furcasternum, since the prothoracic furca invaginates at its posterior edge (Friedrich *et al.* 2009).

12 Profurcal arm and propleura: (0) not connected; (1) not fused, furca and pleural apophysis connected by muscle; (2) furca and pleural apophysis closely fitting (character 11 of Wipfler *et al.* 2015)

In Caelifera the prothoracic furcal arm is frequently united with the cryptopleura that exhibits, in contrast to the majority of the Ensifera, a well-developed pleural arm (Fig. 8F and Snodgrass 1929; Misra 1946; de Zolessi 1968). As a consequence, the muscle Ispm1 (M. profurca-apodemalis of Friedrich & Beutel 2008) is absent in the vast majority of Caelifera (see Supplementary Table 1). Only in the tridactylid *Xya*, the profurcal arm of each body half extends in a posteriodorsal direction, whereby their distal ends are almost touching each other (Fig. 9F).
Within the Ensifera, different character states are present. The profurca of true crickets (Gryllidae) extends in a lateral direction and closely fits the pleural ridge of the cryptopleura (Fig. 7A) (Voss 1905a). This situation is comparable to that reported for the cockroach *Peripaneta* (Carbonell 1947), for which the respective character was coded “2” by Wipfler *et al.* (2015). The prothoracic furca of mole crickets (Gryllotalpidae) is rigidly connected to the cryptopleura, both structures forming a single inflexible unit (Carpentier 1921b). The remaining examined ensiferan species have a freestanding profurca not

reaching close to the pleura. A connection of profurca and propleura by the muscle Ispm1 is present in Tettigoniidae, Anostostomatidae and *Prosopogryllacris*. The respective muscle is absent in *Stenopelmatus*, *Comicus* and *Troglophilus* (see Supplementary Table 1).
In the phasmid *Timema* (Kristensen 1975) and Dermaptera (Günther & Herter 1974), the profurcal arm reaches very close to the prothoracic pleural arm. However, these taxa are additionally characterized by a chitinous connection of both structures. This ligament is likely a vestige of Ispm1, whereby the muscle fibers are no longer present, the ligament itself corresponds to the muscle tendon. Therefore, the character state "1" is herein added for *Timema*, and the character state of the dermapteran *Euborellia* is herein changed to "1". The profurca of the archostematan *Tetraphalerus* is freestanding and no muscle connects its profurca and propleura (Friedrich *et al.* 2009).

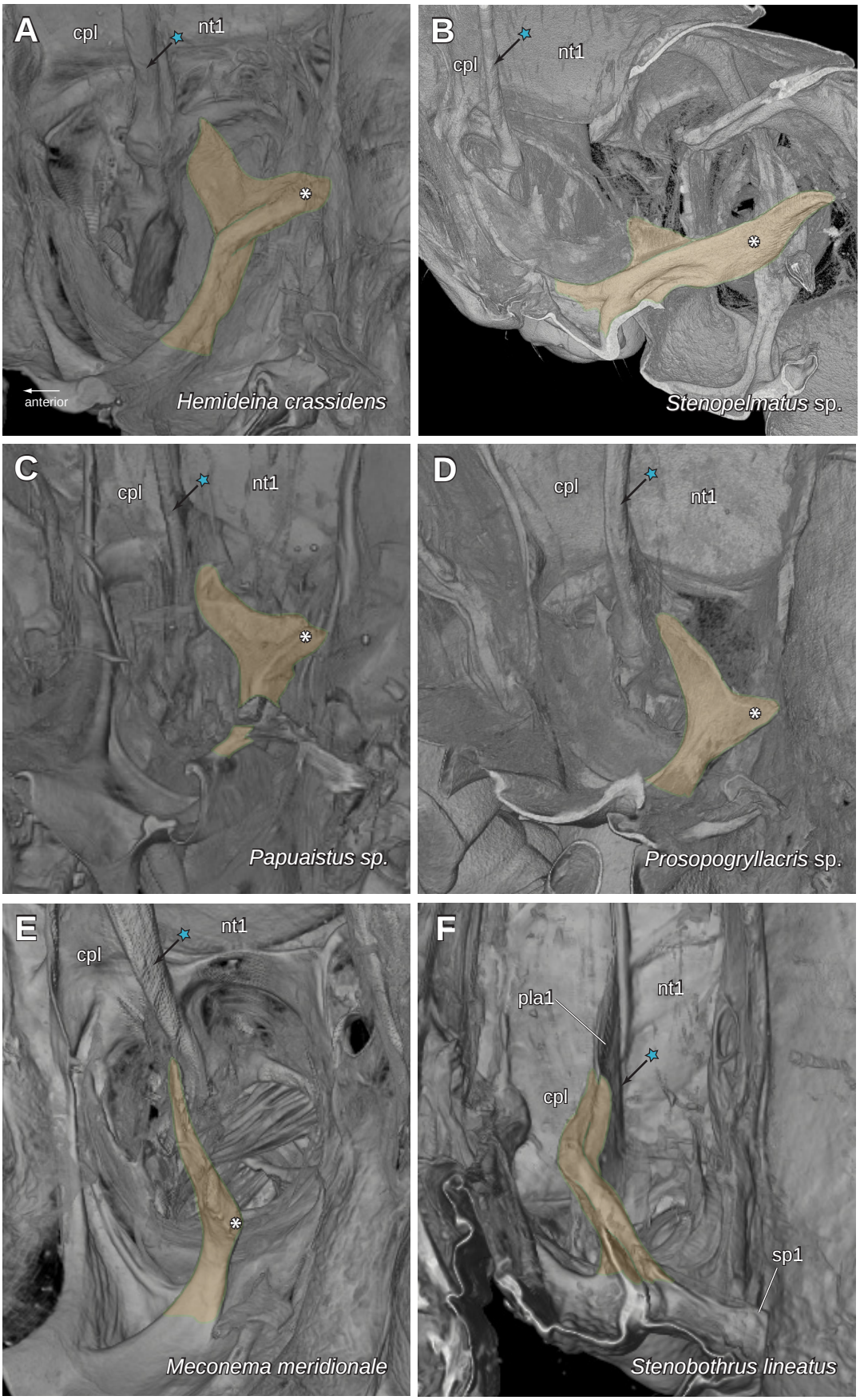
13 Profurca: (0) present; (1) reduced to a minimum or absent (character 10 of Wipfler *et al.* 2015)

A profurca is virtually absent in all Phasmatodea except *Timema* (see Bradler 2009 for detailed information). Character coding adopted from Wipfler *et al.* (2015).

14 Profurca (2): (0) with single furcal arm; (1) branched

In the wide range of Polyneoptera, the prothoracic furca of each body side consists of a single undivided extension, the profurcal arm, which projects in an anterior (*Timema*: Kristensen 1975, Tilgner *et al.* 1999; Zoraptera: Friedrich & Beutel 2008), posterior (Embioptera: Rähle 1970, *Xya* sp.: Supplementary Plate 45), or lateral (most Caelifera: Snodgrass 1929, Albrecht 1953, Blackith and Blackith 1966, de Zolessi 1968; Blattodea incl. Isoptera: Matsuda 1956b, Matsuda 1970, Plecoptera: Wittig 1955; Dermaptera: Günther & Herter 1974; Mantodea: Matsuda 1970) direction. Hence, a non-branched profurca is most likely the plesiomorphic condition for Ensifera. Within the Ensifera, only the cave cricket *Troglophilus* (Leubner *et al.* 2016) and

Figure 8 (see opposite page). Morphology of the prothoracic furca in representatives of Ensifera (A)–(E), and Caelifera (F). Lateral view. Profurca is highlighted in transparent orange. The white asterisk * marks the posterior arm-like or bulbous extension of the profurca. Blue asterisks mark the pleural ridge of cryptopleura. In contrast to (A)–(E), caeliferan representative in (F) has strikingly marked prothoracic pleural arm. Abbreviations: *cpl* cryptopleura, *nt1* pronotum, *pla1* prothoracic pleural arm, *sp1* prospina.


A
cpl
nt1
anterior
Hemideina crassidens
B
cpl
nt1
Stenopelmatus sp.
C
cpl
nt1
Papuaistus sp.
D
cpl
nt1
Prosopogryllacris sp.
E
cpl
nt1
Meconema meridionale
F
pla1
nt1
cpl
sp1
Stenobothrus lineatus

further representatives of the Rhaphidophoridae (Gurney 1935; Richards 1955) have a furca with a single furcal arm in the prothorax. The remaining representatives of Ensifera are characterized by a branched profurca that has an anterior arm-like branch and a posterior branch, which occurs in varying forms (Fig. 8 and character 7). Also Grylloblattodea and Mantophasmatodea have a branched profurca. In contrast to Ensifera, the anterior furcal arm of Grylloblattodea and Mantophasmatodea is bifid near the tip (Walker 1938; Wipfler *et al.* 2015).

In *Siphlonurus* (Ephemeroptera) (Matsuda 1956a), *Phloeothrips* (Thysanoptera) (Mickoleit 1979), and *Palpares* (Neuroptera) (Czihak 1954) the profurca of each body half bears a single arm-like projection. The profurca of *Stenopsocus* (Psocoptera) has a long anterior arm-like projection and a posterior bulbous processus that serves as an insertion point for muscles (Badonell 1934).

In Hymenoptera, the profurca is of varying shape. In most cases the distal part of the single arm is broadened and the furcae of each body side adjoin each other (Vilhelmsen *et al.* 2010). The profurca of the archostematan *Tetraphalerus* bears a short common stem (Friedrich *et al.* 2009). The single laterally oriented furcal arms are very broad, paddle-like extensions, whereby the broad surface is pointing anteriorly (Friedrich *et al.* 2009).

15 Posterior branch of profurca: (0) short processus; (1) bulbous, knob-like extension; (2) arm-like, tapered processus

The posterior branch of the profurca in Grylloblattodea and Mantophasmatodea appears as a short processus easily distinguishable from the furcal stem (Walker 1938; Wipfler *et al.* 2015). In Gryllidae (Fig. 7A) and Tettigoniidae (*Meconema*: Fig. 8E) the profurca has a short slender stem that distally splits in an anterior tapered arm-like processus and a posterior bulbous or knob-like extension. Mole crickets (Gryllotalpidae) also have a bifurcated furca consisting of an anterior and an elongated posterior arm-like processus (Fig. 7B). Schizodactylidae (*Comicus*: Leubner *et al.* 2017, *Schizodactylus*: Khattar 1960), Anostostomatidae (H*emideina* and *Papuaistus*: Fig. 8A, C), Stenopelmatidae (*Stenopelmatus*: Fig. 8B), Gryllacrididae (*Prosopogryllacris*: Fig. 8D), and Prophalangopsidae (*Cyphoderris*: Supplementary Plates 1, 2) are characterized by a branched profurca with a pronounced posterior arm-like processus.

The profurca of *Stenopsocus* (Psocoptera) has a long anterior arm-like projection and a posterior bulbous processus, that serves as an insertion point for muscles (Badonell 1934).

16 Prospina: (0) present; (1) absent (character 12 of Wipfler *et al.* 2015)

A prospina is present in the majority of examined taxa. It is lacking in *Siphlonurus* (Ephemeroptera) (Matsuda 1956a) and *Palpares* (Neuroptera) (Czihak 1954). A prothoracic spina is also absent in the archostematan beetle *Tetraphalerus* (Friedrich *et al.* 2009). Within the Phasmatodea, a prospina is solely present in *Timema* (Tilgner *et al.* 1999; Bradler 2009).

17 Shape of prospina: (0) stick-like, tapered; (1) flat median extension; (2) stalked, with distal plate and/or processi; (3) massive, long, blade-like

In the vast majority of insects, the prospina appears as a stick-like tapered internal protrusion (Matsuda 1970). In contrast to *Timema*, whose prospina is well-developed and stick-like (Tilgner *et al.* 1999), the prospina is virtually absent in the remaining Phasmatodea apart from members of the Aschiphasmatinae (Klug 2008; Bradler 2009b). In most representatives of the Caelifera, the prospina appears as a flat median extension (Fig. 8F) (Snodgrass 1929; Misra 1946; Blackith & Blackith 1966; de Zolessi 1968). Only in the caeliferan *Xya* sp. the prospina is a long and massive structure, extending into the mesothorax (Fig. 9F). As this is not comparable to all of the aforementioned character states, it is treated independently and coded as character state “3”. In contrast, all representatives of the Ensifera are characterized by a prospina that always bears a slim stalk and a distal expansion, formed as a distal plate that might bear lateral, anterior and/or posterior processi (Fig. 9).

18 Stalked prospina: (0) with single posterior processus; (1) with paired posterior processus

The stalked prospina of Ensifera bears several processi serving as attachment points for the well-developed ventral longitudinal musculature. These processi protrude in an anterior, lateral or posterior direction (Fig. 9). In representatives of the Gryllidae (Fig. 7A) and the hump-winged cricket *Cyphoderris* sp. (Fig. 9C) the single posterior processus is rounded and not elongated in a posterior direction. An elongated single

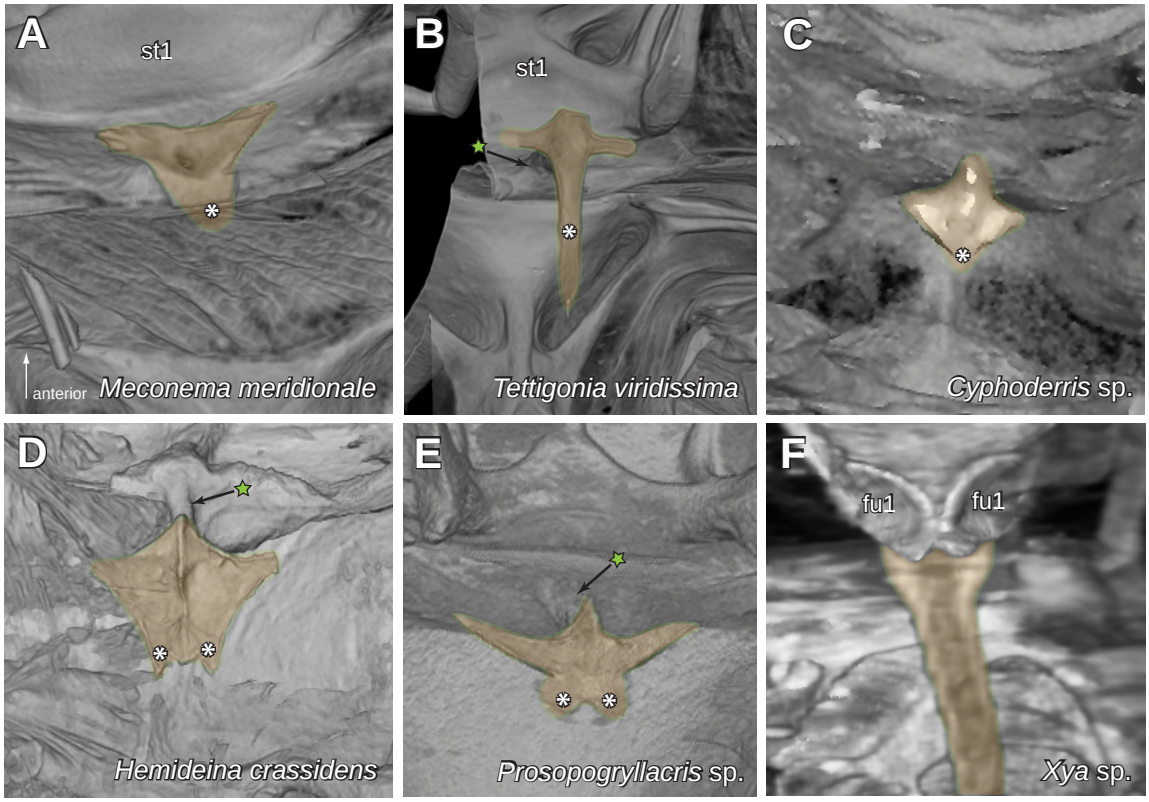


Figure 9. Morphology of the prothoracic spina in representatives of Ensifera (A)–(E), and Caelifera (F). Dorsal view. Prospina is highlighted in transparent orange. The white asterisk * marks the single or paired posterior processus of the prospina. Green asterisks mark visible prospinal stalk. In contrast to (A)–(E), the prospina of the caeliferan representative (F) has a broad basis and is non-stalked. Abbreviation: *fu1* profurca.

median posterior processus of the prospina is present in mole-crickets (Fig. 7B) and all representatives of the Tettigoniidae (Fig. 9A, B). The prospina of Anostostomatidae (*Hemideina*: Fig. 9D), Gryllacrididae (*Prosopogryllacris*: Fig. 9E), Stenopelmatidae (not illustrated), Rhaphidophoridae (Richards 1955; Leubner *et al.* 2016), and Schizodactylidae (Leubner *et al*. 2017; Khattar 1960) bears a paired posterior processus each pointing in a more posterolateral direction.

19 Prospina (0) on posterior part of basisternum or connected with furca (sternum); (1) on distinct spinasternite or lying in membranous area between pro- and mesosternum; (2) on anterior part of mesosternum (adopted and modified from character 13 of Wipfler *et al.* 2015)

In the majority of Ensifera the prospina is situated on a distinct spinasternite situated in the membranous area between the prosternum and mesosternum; in Gryllotalpidae (Fig. 7B),

Anostostomatidae (O'Brien & Field 2001), *Cyphoderris* (Supplementary Plate 2), *Stenopelmatus* sp (Supplementary Plate 33), Gryllacrididae (Ander 1933) and most Tettigoniidae (Naskrecki 2000). In contrast to the opinion of Wipfler *et al*. (2015), a distinct prospinasternum is also found in representatives of the Gryllidae: *Acheta* (Voss 1905a) and *Gryllus* (Supplementary Plate 10). The same situation is found in Grylloblattodea (Walker 1938), Mantophasmatodea (Wipfler *et al.* 2015), Phasmatodea (Jeziorski 1918; Tilgner *et al.* 1999), and some cockroaches (Carbonell 1947; Matsuda 1956b). In contrast to the hypotheses proposed in Wipfler *et al.* (2015), a distinct spinasternite is also found in Dermaptera (Günther & Herter 1974) and Plecoptera (Matsuda 1970). In Rhaphidophoridae, the prospinasternite is externally reduced as an exposed sclerite (Gurney 1935; Richards 1955; Leubner *et al.* 2016), a situation also found in Zoraptera (Friedrich & Beutel 2008), some cockroaches and termites (Crampton 1926). Nevertheless, the prospina is situated in the membranous area between the pro- and mesothoracic sterna in the aforementioned taxa. This distinct separate position of the prospina from basi- and furcasternite implies a homologous condition to the situation found in taxa with a distinct, but separated spinasternite. The character is therefore coded as "1" for these taxa. Only in some Tettigoniidae, e.g. Hetrodinae, Meconematinae and Phaneropterinae, the prospinasternite is fused with the prosternum (Naskrecki 2000), a condition also found in representatives of the Caelifera, namely Acrididae (e.g. Snodgrass 1929; Albrecht 1953), Eumastacidae (Blackith & Blackith 1966) and Proscopiidae (de Zolessi 1968). In Embioptera, the prospina is situated at the posterior end of the prosternum, a distinct prospinasternite is not developed (Rähle 1970). In dune crickets (Schizodactylidae), the prospina is situated close to the anterior edge of the mesosternum on a narrow sclerite that could only be differentiated from the mesosternum via a suture (Leubner *et al.* 2017). Therefore, the prospinasternite (*presternite* of Khattar and Srivastava 1962) and the mesosternum form a single sclerite. This condition is not comparable to that found in all other examined taxa, and is therefore coded as a unique character state.

A prothoracic spinasternite could not be identified in *Tetraphalerus* (Friedrich *et al.* 2009), a prothoracic spina is absent. In the approach of Wipfler *et al.* (2015) the character was coded "not applicable" for all representatives without a prospina (*Siphlonurus*, *Megacrania*, *Palpares*). This opinion is followed herein and the respective character is likewise coded inapplicable for the archostematan beetle *Tetraphalerus*.

20 Median mesonotal suture: (0) absent; (1) present (character 14 of Wipfler *et al.* 2015)
In *Tetraphalerus*, a median suture of the mesonotum is not mentioned, but internally there is a median ridge starting at the porsterior face of the prophragma stretching posterad across half of the mesonotal total length (Friedrich *et al.* 2009). Nonetheless, the homology to the median mesonotal suture of other taxa, e.g. Hymenoptera (Vilhelmsen 2000) or Plecoptera (Matsuda 1970), is unclear, the character is coded as "?" for the archostematan *Tetraphalerus*. Character coding for remaining taxa adopted from Wipfler *et al.* (2015).

21 Pleural arm of mesothorax: (0) absent; (1) present (character 15 Wipfler *et al.* 2015)
A mesothoracic pleural arm is present in the majority of examined taxa, including all representatives of the Orthoptera (e.g. Fig. 10, Supplementary Plate 32) and the archostematan beetle *Tetraphalerus* (Friedrich *et al.* 2009). Character coding for remaining taxa adopted from Wipfler *et al.* (2015).

22 Pleural arm of mesothorax (2): (0) small processus; (1) arm-like structure projecting in thoracic cavity; (3) large, plate-like (adopted and modified from character 16 of Wipfler *et al.* 2015)
The pleural arm appears as a small processus in *Grylloblatta* (Grylloblattodea)(Walker 1938), *Euborellia* (Dermaptera) (Bharadwaj & Chadwick 1974a), *Zorotypus* (Zoraptera) (Friedrich & Beutel 2008), all phasmatodeans except *Timema* (Klug 2008), *Macroxyela* (Hymenoptera) (Vilhelmsen *et al.* 2010) and *Palpares* (Neuroptera) (Czihak 1957). *Periplaneta* (Blattodea) and *Stagmomantis* (Mantodea) have broad pleural arms which reach far into the thoracic cavity (Carbonell 1947; Levereault 1936), a situation also observed in the remaining taxa including the orthopteran representatives (e.g. Supplementary Plates 11, 25, 32). In *Tetraphalerus* (Archostemata) the mesopleural arm is large and plate-like (Friedrich *et al.* 2009), a condition not comparable to the remaining taxa.

23 Invagination of of mesopleural arm: (0) near the middle of the pleural ridge; (1) ventrad in direct proximity to the pleural condylus articulating with the coxa; (2) posterad to the pleural ridge, internal processus of epimeron (adopted and modified from character 17 of Wipfler *et al.* 2015)

The position of the meso- and metathoracic pleural arm, an internal protrusion of the pleural ridge, is differing within the Polyneoptera. In Dermaptera (Matsuda 1970; Bharadwaj & Chadwick 1974a), Zoraptera (Friedrich & Beutel 2008) and Plecoptera (Wittig 1955; Matsuda 1970) the pleural arm arises near the middle of the pleural ridge. In contrast, the pleural arm of Orthoptera (Ensifera: Supplementary Plates 8, 11, 25; Caelifera: Supplementary Plate 32), Blattodea incl. Isoptera (Matsuda 1970; Weidner 1970a), and Mantodea (Matsuda 1970) originates ventrad at the pleural ridge in direct proximity to the pleural condylus that articulates with the coxa. Also in Euphasmatodea, a short processus is located on the pleural ridge near the pleurocoxal articulation and is homologized with the pleural arm of other polyneopteran taxa (Klug 2008). In *Timema*, the pleural ridge is only weakly sclerotized and sail-shaped bearing no internal protrusion, a pleural arm is absent (Klug 2008). The pleural arm is likewise absent in the meso- and metathorax of Embioptera (Barlet 1985c; Klug 2008). In Grylloblattodea (Walker 1938) and Mantophasmatodea (Wipfler *et al.* 2015), the pleural arm of the meso- and metathorax is situated posterior to the pleural ridge and is assumed to be an internal processus of the epimeron.

The pleural arm of Thysanoptera invaginates in the ventral half of the pleural ridge, but it lies not in direct proximity to the pleural condylus (Matsuda 1970; Mickoleit 1979). The character is therefore coded as "?". In Hymenoptera, the pleural arm extends in some cases from the anterodorsal edge of the episternum (Vilhelmsen *et al.* 2010), a situation herein homologized to character state "0". In *Tetraphalerus* (Archostemata), only the mesothoracic pleural arm is developed (Friedrich *et al.* 2009). It is situated in the anterior half of the internal pleural ridge (Friedrich *et al.* 2009).

24 Position of pterothoracic furcae in relation to corresponding pleural arm: (0) free-standing, not situated directly ventrad of pleural arm; (1) enclosing pleural arm from ventral side

Exclusively in both subtaxa of Orthoptera, Caelifera (Fig. 10C) (Snodgrass 1929; Misra 1947; de Zolessi 1968) and Ensifera (Fig. 10A, B) (Voss 1905a, d; Carpentier 1936) this apophysis forms a shelf at its free end to accommodate the pleural apophysis of the corresponding body side to which it is moveably attached by a sternopleural muscle (IIspm2). In the remaining taxa the pterothoracic furca appears as a free-standing internally protruding

apophysis that is not in contact and/or direct relation to the pleural arm (Badonell 1934; Matsuda 1956b; Matsuda 1970; Tilgner *et al.* 1999; Klug 2008; Vilhelmsen *et al.* 2010). This character is not applicable to taxa without a pleural arm.

25 Mesosternum: (0) externally exposed; (1) invaginated (character 18 of Wipfler *et al* . 2015)

The ventral mesothoracic sclerite of holometabolan insects, termed mesoventrite, is mainly composed of pleural elements. The sternal part of the ventrite is limited to a narrow median invaginated carina (Beutel *et al.* 2011). All other taxa have an externally exposed sternum (basisternite) (Beutel *et al.* 2011).

26 Ventral mesosternal processus (below mesofurca) forming sternocoxal joint: (0) absent; (1) present (character 19 of Wipfler *et al.* 2015)

A ventral mesosternal processus only occurs in Holometabola (Matsuda 1970), but is absent in Coleoptera (Friedrich *et al.* 2009) and Strepsiptera (Koeth *et al.* 2012). Character coding adopted from Wipfler *et al.* (2015).

27 Anterior processus of mesofurcal arm: (0) absent, (1) present

In the vast majority of Polyneoptera, each mesofurcal arm of each body side appears as an unfurcated elongated apophysis that extends in a lateral direction, as it is documented for Grylloblattodea (Walker 1938), Embioptera (Barlet 1985d; Klug 2008), Phasmatodea (Tilgner *et al.* 1999; Klug 2008), Mantodea (Matsuda 1970), Blattodea (Matsuda 1956b), and Plecoptera (Matsuda 1970). Correspondingly, the mesofurcal arm of Ensifera appears as a lateral projection that bears no anterior processus (Fig. 10). In contrast, the mesofurcal arm of Caelifera is characterized by an anteriorly directed processus (Fig. 10C, F) (Snodgrass 1929; Misra 1947; de Zolessi 1968). An additional characteristic of the anterior mesofurcal processus in Caelifera is that it serves as an insertion point for the ventral longitudinal muscles Ivlm7 (*M. profurca-mesofurcalis*) and Ivlm9 (*M. prospina-mesofurcalis*). In Ensifera, where the anterior processus is absent, both muscles insert at the anterior edge of the mesofurcal arm (Fig. 10A, B). An anterior mesofurcal processus serving as an insertion point for Ivlm7 (Ivlm9 is absent) is also reported for Mantophasmatodea (Wipfler *et al.* 2015). The state of this character in Zoraptera and Dermaptera is unsure.

Whereas no concrete description is available for the morphology of the mesofurca, an anterior protrusion is recognizable in the illustrations of Zoraptera (Fig. 6C in Friedrich & Beutel 2008) and Dermaptera (Fig. 14b in Kleinow 1966).

The mesofurca of the mayfly *Siphlonurus* (Matsuda 1956a) and the thrip *Phloeothrips* (Mickoleit 1979) bears a single arm-like projection. In *Stenopsocus* (Psocoptera) (Badonell 1934) and *Palpares* (Neuroptera) (Czihak 1954) a short anterior processus is present that serves as an insertion point for the mesofurcal-profurcal muscles (*Ivlm7*).

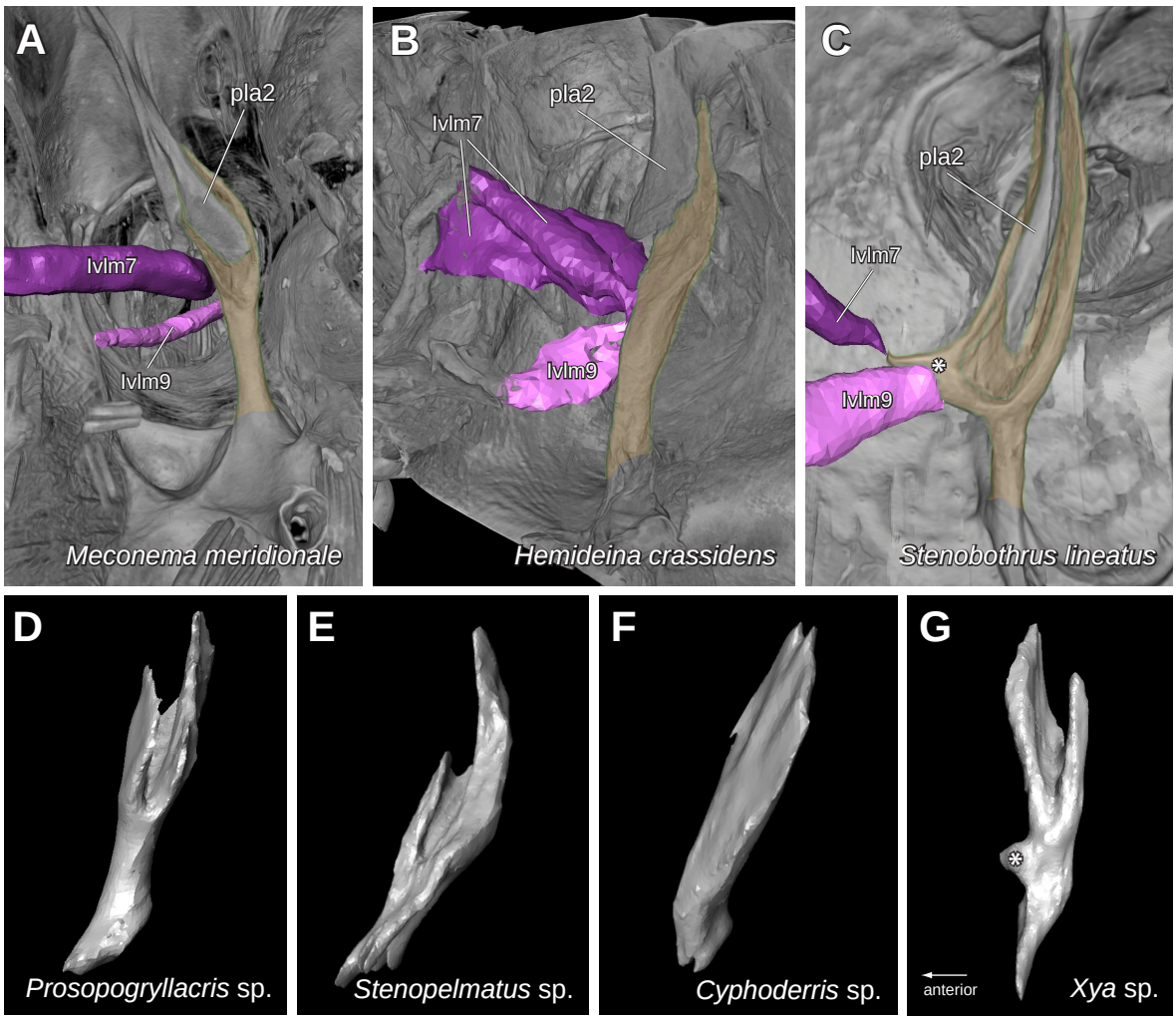


Figure 10. Morphology of the mesothoracic furca in representatives of Ensifera (A, B, D–F) and Caelifera (C, G). (A)–(C) Volume rendering of mesothorax showing ventral longitudinal muscles inserting at anterior process * or anterior edge of mesofurca. Mesofurca is enclosing the pleural arm from ventral side. (D)–(G) 3D-reconstruction of mesofurcae. In contrast to ensiferan representatives, the mesofurca of the caeliferan *Xya* sp. (G) bears an anterior process *. The muscles Ivlm7 (M. profurca-mesofurcalis) and Ivlm9 (M. prospina-mesofurcalis) insert at anterior processus. Abbreviation: *pla2* mesothoracic pleural arm.

In Hymenoptera, the structure of the mesofurca can be very complex (Vilhelmsen *et al.* 2010), but an anterior processus is not developed. The mesofurca of the archeostematan beetle *Tetraphalerus* is a single, unfurcated arm-like extension broadened at its distal end (Friedrich *et al.* 2009).

28 Mesospina: (0) present; (1) absent (character 21 of Wipfler *et al.* 2015)

A mesospina is present in the majority of examined taxa. However, it is absent in *Siphlonurus* (Ephemeroptera) (Matsuda 1956a), *Phloethrips* (Thysanoptera) (Mickoleit 1979) and *Palpares* (Neuroptera) (Czihak 1954). A chitinous bridge between the bases of the mesofurcal arms is homologized with the mesospina in *Stenopsocus* (Psocoptera) (*pont de chitine molle* in Badonell 1934). In the phasmid *Timema* a mesospina is present (Tilgner *et al.* 1999; Bradler 2009). Apart from members of the Aschiphasmatinae, the mesospina is lacking in Euphasmatodea (Bradler 2009b). Although the mesospina is absent in many representatives of the Hymenoptera, it is present in the sawfly *Macroxyela* (Vilhelmsen 2000). Character coding adopted from Wipfler *et al.* (2015).

29 Position of mesospina: (0) on distinct spinasternite; (1) on posterior part of basisternite; (adopted and modified from character 22 of Wipfler *et al.* 2015)

The mesospina is an internal protrusion of the spinasternite (Snodgrass 1935). Usually, the spinasternite forms an independent sclerite that is clearly separated by a membranous area and is situated posterior to the mesothoracic furca- and/or basisternite, e.g. in Grylloblattodea (Walker 1938), Blattodea (Matsuda 1956b), Mantodea (Matsuda 1970), *Timema* (Tilgner *et al.* 1999), Embioptera (Barlet 1985c), Dermaptera (Bharadwaj & Chadwick 1974b). In other taxa, no distinct spinasternite is developed. Instead it is indistinguishably fused with the basi- and furcasternite. This is the case in all representatives of the Orthoptera (Beier 1972), in Mantophasmatodea (Wipfler *et al.* 2015), Plecoptera (Matsuda 1970), Hymenoptera (Vilhelmsen *et al.* 2010), and Archostemata (Friedrich *et al.* 2009).

The situation in *Zorotypus* (Zoraptera) is unclear, because no distinct spinasternite is developed, but the authors did not mention the concrete position of the mesospina in relation to other sclerites (Friedrich & Beutel 2008). In *Stenopsocus* (Psocoptera), the mesospina appears as a chitinous bridge between the furcal bases (see character 28 and

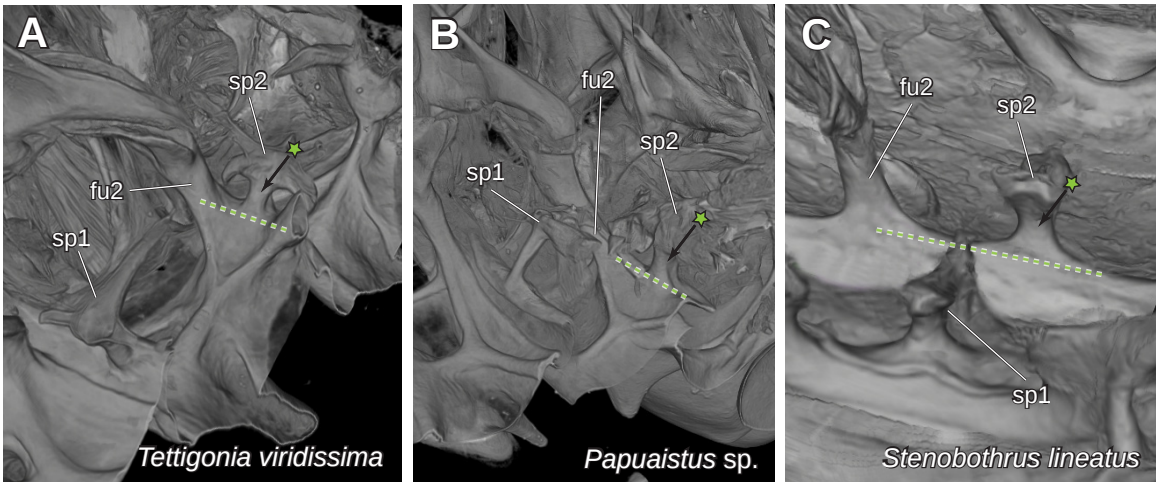


Figure 11. Position of mesospina in relation to furcal origin. In representatives of Ensifera (A, B) and Caelifera (C) both structures are arranged in one line (dashed line). The mesospina is characterized by a short stalk (marked by green asterisk) and distal plate with (A, B) or without (C) processi. Abbreviations: *fu2* mesofurca, *sp1/2* pro-/mesothoracic spina.

Badonell 1934). Since the spina is thereby in close association with the furcasternite, the character is coded "1" for *Stenospocus*.

30 Position of mesospina in relation to furcal origin: (0) posterior to origin of mesofurcae; (1) mesospina and mesofurcae situated in one line on a single horizontal internal ridge (sternacosta)

In the vast majority of insects, the mesopina is situated posterior to the furcal origin. Also in those taxa, in which the spinasternite is fused with the basi- and furcasternite, the mesospina is always situated posterior to the origin of the mesofurca (e.g. in Mantophasmatodea, Wipfler *et al.* 2015). In contrast, the mesospinasternite of Orthoptera is indistinguishably fused with the furcasternite (Beier 1972). Internally, the bases of the furcae are connected through a sclerotized ridge, the sternacosta (Snodgrass 1935). In Orthoptera, the mesospina is situated on the sternacosta, medially between the bases of the mesofurca. Thereby all three apophyses lie in one line within the mesothorax (Fig. 11). For Hymenoptera, the situation cannot be homologized and is coded as "?", since the mesospina, when developed, is situated between the furcal bases, but a sternacosta is never developed (Vilhelmsen 2000).

31 Shape of mesospina: (0) spine- or knob-like; (1) stalked, with distal plate and/or processi

In insects, the unpaired median protrusion of the mesothorax, the mesospina, is mainly of simple, and spine-like, tapered or knob-like shape, without bearing any processi (Dermaptera: Barlet 1985c; Mantophasmatodea: Wipfler *et al.* 2015; Grylloblattodea: Walker 1938; Blattodea and Isoptera: Matsuda 1956b, 1970; Mantodea: Matsuda 1970; *Timema*: Tilgner *et al*. 1999; Zoraptera: Friedrich & Beutel 2008; Plecoptera: Wittig 1955; Embioptera: Barlet 1985a). This situation is also documented for the archostematan beetle *Tetraphalerus* (Friedrich *et al.* 2009) and the sawfly *Macroxyela* (Vilhelmsen 2000). However, the mesospina of representatives of the Caelifera bears a short stalk, is flattened at its distal part, fin-shaped and oriented along the longitudinal axis (Figs. 11C, 12M and e.g. Albrecht 1953; Blackith and Blackith 1966; de Zolessi 1968). The mesospina of Ensifera is likewise stalked, but just as in the prothorax it bears several processi at its distal plate (Fig. 12A–L).

32 Distal part of stalked mesospina: (0) without processi; (1) with processi

As stated above, only members of both subtaxa of Orthoptera have a stalked mesospina. The distal part of the mesospina of Caelifera is flattened, fin-shaped and oriented along the longitudinal axis (Misra 1947; Blackith & Blackith 1966; de Zolessi 1968). All examined Ensifera have a stalked mesospina that bears a number of processi at its distal part (Fig. 12A–L). As previously stated by Naskrecki (2000) the secondary structure of the mesospina provides several characteristics potentially revealing the internal systematics of Tettigoniidae. In his study, the author distinguishes between an unpaired anterior and posterior processus, paired ventrolateral ones and paired dorsolateral processi as substructures of the mesospina. Actually, the secondary structure of the mesospina shows some specific features that might be useful to reveal the higher phylogenetic relationships of Ensifera.

33 Lateral processi of stalked mesospina: (0) mesospina with paired processi, ventrolateral and dorsolateral per body side; (1) mesospina only with a single laterally processus per body side, T-shaped

Almost all examined ensiferan taxa bear a mesospina with paired lateral processi, one pointing in a dorsolateral the other in a ventrolateral direction (Fig. 12A–E, G–L). Only

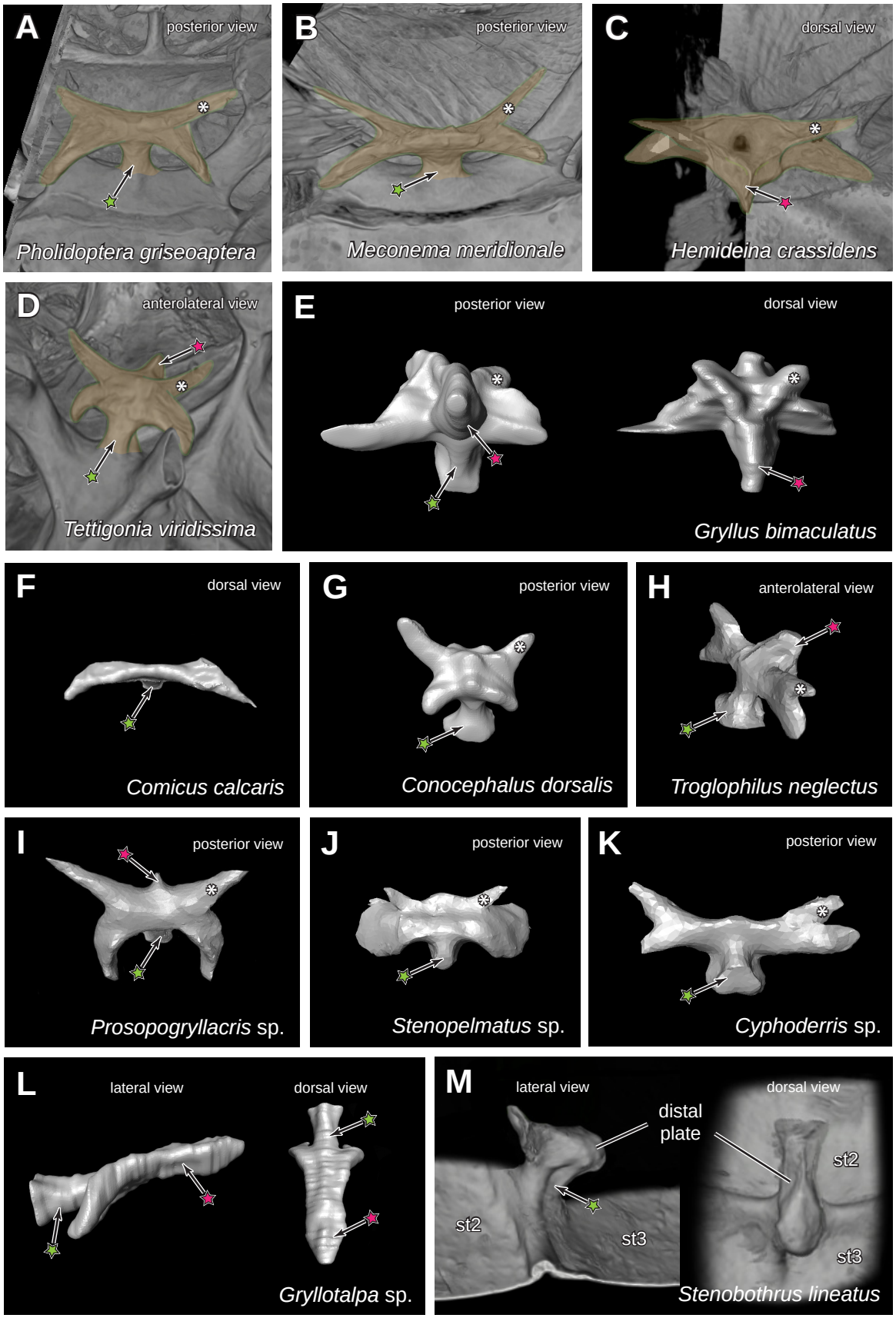
in members of the Schizodactylidae, namely *Comicus* (Fig. 12F) and *Schizodactylus* (Khattar & Srivastava 1962) a single lateral processus is present giving the mesospina a T-shaped appearance. The mesospina of mole crickets (Gryllotalpidae) was reported to be a massive, rodshaped structure, that reaches far into the metathorax (Carpentier 1936). In contrast, through the investigation of µCT-data it could be figured out, that the mesospina of *Gryllotalpa* bears a short stalk, ventrally oriented lateral processi and a single elongated posterior processus (Fig. 12L).

34 Shape of dorsolateral processus of mesospina: (0) tapered, arm-like; (1) bulbous, knob-like

The dorsolateral processus of the mesospina appears as a tapered, arm-like extension in the vast majority of Ensifera (Fig. 12). Only in members of the Gryllidae, the dorsolateral processus is knob-like (Fig. 12E and Voss 1905a). The homology of the single lateral processus present in dune crickets (Schizodactylidae) and mole-crickets (Gryllotalpidae) with the ventral or dorsal lateral processus is unsure, the character is therefore coded as "?" for these taxa.

In subsequent studies including more representatives of ensiferan subtaxa like Jerusalem crickets (Stenopelmatidae), wetas and king crickets (Anostostomatidae), and raspy crickets (Gryllacrididae), there should also be paid attention to the morphology of the ventrolateral processus. As shown in Fig. 12, this processus shows tremendous morphological differences between the examined ensiferan taxa. For example, the ventrolateral processus of *Stenopelmatus* (Fig. 12J) is rounded, that of *Prosopogryllacris* (Fig. 12I) is strongly bent towards the ventral side. Since these characteristics could merely be autapomorphies of the concerning species, the structure of the ventrolateral processus of the mesospina is not coded as a character in the present study.

The presence of a posterior processus of the mesospina is documented for some representatives of Ensifera: the anostostomatids *Hemideina* (Fig. 12C) and *Papuaistus* (not figured), the katydid *Tettigonia* (Fig. 12D), the cricket *Gryllus* (Fig. 12E), the mole cricket *Gryllotalpa* (Fig. 12L) and the cave cricket *Troglophilus* (Fig. 12H). Regarding this current data basis on only a few ensiferan taxa, the presence of this processus as well as


A
posterior view
Pholidoptera griseoaptera
B
posterior view
Meconema meridionale
C
dorsal view
Hemideina crassidens
D
anterolateral view
Tettigonia viridissima
E
posterior view
dorsal view
Gryllus bimaculatus
F
dorsal view
Comicus calcaris
G
posterior view
Conocephalus dorsalis
H
anterolateral view
Troglophilus neglectus
I
posterior view
Prosopogryllacris sp.
J
posterior view
Stenopelmatus sp.
K
posterior view
Cyphoderris sp.
L
lateral view
dorsal view
Gryllotalpa sp.
M
lateral view
distal plate
st2
st3
dorsal view
st2
st3
Stenobothrus lineatus

its secondary structure (e.g. blade-like, knob-like or tapered) are not coded as characters in the present study.

35 Mesocoxae: (0) separated from each other by a distinct gap; (1) closely adjacent medially (character 20 of Wipfler *et al.* 2015)

Only in Holometabola the mesocoxae are closely adjacent, due to the modifications of the sternal region (Beutel *et al.* 2011). Character coding adopted from Wipfler *et al.* (2015).

36 Pleural arm of metathorax: (0) absent; (1) present (character 24 of Wipfler *et al.* 2015)

The state of this character is the same as in character 21 for all investigated species, with the exception of the archostematan beetle *Tetraphalerus*. In *Tetraphalerus*, only the mesopleural arm is developed, a metapleural arm is absent (Friedrich *et al.* 2009).

37 Pleural arm of metathorax: (0) small processus; (1) arm-like structure projecting in thoracic cavity (character 25 of Wipfler *et al.* 2015)

With the exception of the archostematan beetle *Tetraphalerus*, where this character is not applicable, the coding is the same as in character 22. Character coding adopted from Wipfler *et al.* (2015).

38 Invagination of of metapleural arm: (0) near the middle of the pleural ridge; (1) ventrad in direct proximity to the pleural condylus articulating with the coxa; (2) posterad to the pleural ridge, internal processus of epimeron (adopted and modified from 26 of Wipfler *et al.* 2015)

With the exception of the archostematan beetle *Tetraphalerus*, where this character is not applicable, the coding is the same as in character 23. Character coding adopted from Wipfler *et al.* (2015).

Figure 12 (see opposite page). Morphology of mesospina in representatives of Ensifera (A)-(L) and Caelifera (M). (A)–(D) Volume rendering. (E)–(M) 3D-reconstruction. Orthoptera bear a stalked mesospina (green asterisk). The vast majority of Ensifera is characterized by a mesospina that bears paired dorsolateral* and ventrolateral processi, only *Comicus calcaris* has a single lateral process (F). Whereas the dorsolateral processus* is tapered in most Ensifera, the dorsolateral process* in *Gryllus bimaculatus* is knob-like (E). Some taxa have an unpaired posterior process, marked by pink asterisk. The mesospina of *Stenobothrus lineatus* is characterized by a dorsal plate that lacks processi.

39 Metasternum: (0) externally exposed; (1) invaginated (character 28 of Wipfler *et al.* 2015)

Like in the mesothorax, the ventral skeleton of Holometabola is strongly modified (Beutel *et al.* 2011). See character 25 for further information. Character coding adopted from Wipfler *et al.* (2015).

40 Ventral metasternal processus (below metafurca) forming sternocoxal joint: (0) absent; (1) present (character 29 of Wipfler *et al.* 2015)

As in the mesothorax a ventral metasternal processus only occurs in Holometabola (Beutel *et al.* 2011), but is absent in Coleoptera (Friedrich *et al.* 2009) and Strepsiptera (Koeth *et al.* 2012). Character coding adopted from Wipfler *et al.* (2015).

41 Metasternum and first abdominal sternum: (0) separated, (1) fused (character 30 of Wipfler *et al.* 2015)

In Phasmatodea, the metasternum and first abdominal sternum are fused (see Klug 2008 and Bradler 2009 for details). Character coding adopted from Wipfler *et al.* (2015).

42 Shape of metafurca: (0) single lateral or posterior arm-like extension; (1) furcated

The metathoracic furca appears as an unfurcated laterally or posteriorly oriented arm-like extension in the vast majority of Polyneoptera (Grylloblattodea: Walker 1938; Zoraptera: Friedrich & Beutel 2008; Embioptera: Barlet 1985b, Klug 2008; Phasmatodea: Tilgner *et al.* 1999, Klug 2008; Mantodea: Matsuda 1970; Blattodea: Matsuda 1956b, Beier 1974; Isoptera: Matsuda 1970, Weidner 1970b; Plecoptera: Wittig 1955, Matsuda 1970). The described situation is also found in the mayfly *Siphlonurus* (Matsuda 1956a), the thrip *Phloeothrips* (Mickoleit 1979), and the antlion *Palpares* (Czihak 1954). Besides the laterally oriented arm-like extension, the metafurca of Mantophasmatodea (Wipfler *et al.* 2015) bears an additional anterior processus that serves as an insertion point for ventral longitudinal muscles, namely IIvlm3 (*M. mesofurca-metafurcalis*) and IIvlm5 (*M. mesospina-metafurcalis*). This situation is also found in *Euborellia* (Dermaptera) (Bharadwaj & Chadwick 1974a,b). The sawfly *Macroxyela* (Hymenoptera) has a metafurca bearing a long anterior processus and a short lateral processus (Vilhelmsen 2000). In *Stenopsocus* (Psocoptera), the metafurcal arms, an anterior and a posterior one, are oriented along

the longitudinal axis, a laterally oriented arm is not present (Badonell 1934). In the archostematan beetle *Tetraphalerus*, the small metafurca is composed of laterally oriented arms in addition to anterior arms that are fused proximally and continuous with the tendons of the ventral longitudinal muscles IIvlm3 and IIvlm5. The bases of the lateral arms are broadened, but the distal parts are slender (Friedrich *et al.* 2009).
Within the Orthoptera the metafurca is composed of an obligate lateral processus, only some representatives bear an additional anterior processus. The metafurca of the tridactylid *Xya* sp. is strongly curved and spatulate accommodating the pleural arm, an anterior processus is absent (Fig. 13N). In addition to a laterally oriented furcal arm, the metafurca of Eumastacidae (Blackith & Blackith 1966), Proscopiidae (de Zolessi 1968) and representatives of the Acrididae bears an anterior processus (Fig. 13M and e.g. Snodgrass 1929; Misra 1947; Albrecht 1953). An anterior metafurcal processus is also present in the majority of Ensifera (Fig. 13B–L). Within the Ensifera, only the metafurca of Gryllidae lacks an anterior processus (Fig. 13A and Voss 1905a).

43 Anterior processus of metafurcal arm: (0) tapered, conical; (1) triangular, forming transition to lateral furcal arm

The anterior metafurcal processus of Mantophasmatodea (Wipfler *et al.* 2015), Dermaptera (Bharadwaj & Chadwick 1974b), Psocoptera (Badonell 1934), Hymenoptera (Vilhelmsen *et al.* 2010), and Coleoptera (Friedrich *et al.* 2009) is of conical shape becoming narrower to the distal end. If present, the anterior processus of the metafurcal arm of Ensifera is of the same form (Fig. 13B–L). To the contrary, in the caeliferan representatives Eumastacidae (Blackith & Blackith 1966), Proscopiidae (de Zolessi 1968), and members of the Acrididae (Snodgrass 1929; Misra 1947; Albrecht 1953) the lateral metafurcal arm and its anterior processus merge smoothly into each other. The anterior processus is thereby having a triangular shape (Fig. 13M).

44 Lateral processus of metafurca: (0) arm-like, tapered, conical or flat extension; (1) strongly curved, spatulate, opening oriented dorsally; (2) wing-like, bent, opening oriented anteriorly; (3) broad, tapering dorsolaterally projecting plate

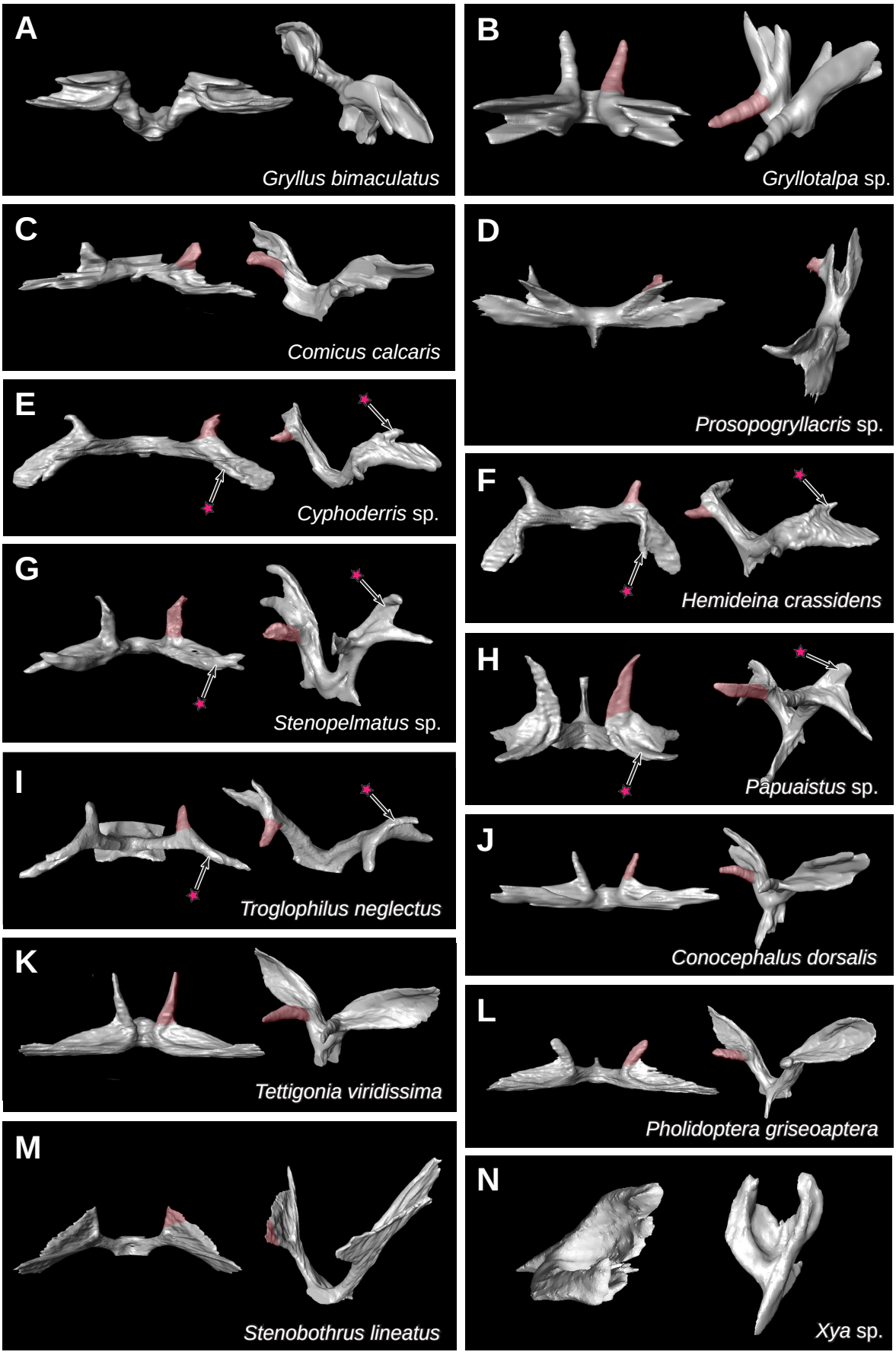
In most of the investigated taxa, the lateral processus of the metafurca appears as an arm-like or flat extension. This situation is reported for Mantophasmatodea (Wipfler *et*

al. 2015), Grylloblattodea (Walker 1938), Dermaptera (Bharadwaj & Chadwick 1974b), Zoraptera (Friedrich & Beutel 2008), Embioptera (Barlet 1985d; Klug 2008), Phasmatodea (Tilgner *et al.* 1999; Klug 2008), Mantodea (Matsuda 1970), Blattodea (Matsuda 1956b; Beier 1974), Isoptera (Matsuda 1970; Weidner 1970a), Plecoptera (Wittig 1955; Matsuda 1970), Ephemeroptera (Matsuda 1956a), Thysanoptera (Mickoleit 1979), Neuroptera (Czihak 1954), and Archostemata (Friedrich *et al.* 2009).

The lateral processus of the metafurca has a different shape in Caelifera and within the Ensifera. Thereby, the threedimensional reconstruction enables a significantly more detailed description of the secondary structure of the metafurca of Orthoptera. In Tridactylidae (*Xya*: Fig. 13M), Gryllidae (*Gryllus*: Fig. 13A; *Acheta*: Voss 1905a), Gryllotalpidae (*Gryllotalpa*: Fig. 13B and Carpentier 1936), and Gryllacrididae (*Prosopogryllacris*: Fig. 13D) the lateral processus of the metafurca is strongly curved and spatulate, building an enclosing shelf for the pleural arm. The lateral metafurcal process forms a flat projection in Anostostomatidae (*Hemideina*: Fig. 13F); *Papuaistus*: Fig. 13H), Schizodactylidae (*Comicus*: Fig. 13C; *Schizodactylus*: Khattar & Srivastava 1962) and Prophalangopsidae (*Cyphoderris*: Fig. 13E). The lateral metafurcal processus in Stenopelmatidae (*Stenopelmatus*: Fig. 13G) and Rhaphidophoridae (*Troglophilus*: Fig. 13I) is more tapered and of conical shape. In the representatives of Tettigoniidae (Fig. 13J–L) the lateral metafurcal processus is wing-like, slightly bent along the dorsoventral axis, the opening oriented in an anterior direction. In the examined representatives of the Acrididae, the lateral metafurcal arm is a broad tapering plate projecting into a dorsolateral direction (Fig. 13M and e.g. Snodgrass 1929; Misra 1947; Albrecht 1953). Since there is no detailed description of the secondary structure of the metathoracic furca for Eumastacidae (Blackith & Blackith 1966) and Proscopiidae (de Zolessi 1968) the respective character is coded as "?".

The situation for the sawfly *Macroxyela* (Hymenoptera) is unclear. According to Vilhelmsen (2000) its metafurca bears a short lateral processus, but it is not illustrated. The character is therefore coded as "?".

Figure 13 (see opposite page). Morphology of metafurca in Ensifera (A)–(L) and Caelifera (M), (N). 3D-reconstruction. Metafurca in dorsal and anterolateral view. An anterior furcal process, shaded in red, is present in the vast majority of Ensifera. Whereas the anterior furcal process is rod-shaped and tapered in representatives of the Ensifera, it forms a transition to the lateral furcal arm in the Caeliferan representative *Stenobothrus lineatus* (M). A dorsal furcal process, marked by pink asterisks, is present only in some ensiferan taxa (E)–(I).


A
Gryllus bimaculatus
B
Gryllotalpa sp.
C
Comicus calcaris
D
Prosopogryllacris sp.
E
Cyphoderris sp.
F
Hemideina crassidens
G
Stenopelmatus sp.
H
Papuaistus sp.
I
Troglophilus neglectus
J
Conocephalus dorsalis
K
Tettigonia viridissima
L
Pholidoptera griseoaptera
M
Stenobothrus lineatus
N
Xya sp.

45 Dorsal processus of metafurca: (0) absent; (1) present

Only within the Ensifera, an additional dorsal metafurcal processus is present in some taxa. In addition to the anterior conical processus and the lateral arm-like extension, the metafurca of these taxa bears a posterolaterally (or dorsolaterally) oriented processus. As a result, the metafurca is triramous in these representatives. The described situation is found in Prophalangopsidae (*Cyphoderris*:Fig. 13E), Anostostomatidae (*Hemideina*: Fig. 13F; *Papuaistus*: Fig. 13H), Stenopelmatidae (*Stenopelmatus*: Fig. 13G), and Rhaphidophoridae (*Troglophilus*: Fig. 13I). A triramous metafurca is likewise reported for additional representatives of the Anostostomatidae, *Anabropsis* sp. (Naskrecki 2000) and another species of *Hemideina* (Maskell 1927), and Rhaphidophoridae, namely *Diestrammena* (Carpentier 1921a, 1923), *Ceuthophilus* (Gurney 1935) and *Macropathus* (Richards 1955).

46 Metaspina: (0) absent; (1) present (character 27 of Wipfler *et al.* 2015)

A metaspina is absent in all studied specimens with the exception of *Grylloblatta* (Grylloblattodea) (Walker 1938). In *Stenopsocus* (Psocoptera), Badonell (1934) homologizes a ridge posterior to the metafurca with the metaspina, following the opinion of Wipfler *et al.* (2015) herein coded as “1”.

47 Metacoxae: (0) separated from each other by a distinct gap; (1) closely adjacent medially (character 31 of Wipfler *et al.* 2015)

As in the mesothorax (character 36), closely adjacent metacoxae only occur in Holometabola (Beutel *et al.* 2011). Character coding adopted from Wipfler *et al.* (2015).

Characters of the thoracic musculature

The homologization of the thoracic musculature of the examined species largely follows the nomenclature established by Friedrich & Beutel (2008). Muscles and muscle characters not defined by Friedrich and Beutel are herein characterized and thoroughly defined. The characters were coded according to the homologization provided in Supplementary Table 1 (see also character matrices in Supplementary Table 2).

Following the definition of Leubner *et al.* (2016), a thoracic muscle is treated as an individual muscle when both origin and insertion and, in addition, the function of this

specific muscle are different from other thoracic muscles found in the thorax. Muscles that have several bundles are characterized through differently originating muscle parts running together in one tendon at a common insertion point. On the other hand, muscles can run parallel but their origin and insertion is clearly separated nonetheless having the same function. These muscles are treated as derivatives of a single muscle and subsequently termed duplicated, multiplicated etc.

The thoracic skeleton and musculature of orthopteran taxa investigated by author of the present study is figured in the supplement (Supplementary Plates 1–45). In the following, some of these are exemplarily given to illustrate the individual muscles that were used in the analysis.

Neck and Prothorax

48 Idlm5 (M. pronoto-phragmalis anterior): (0) absent; (1) present

Present in the vast majority of investigated taxa including all representatives of the Ensifera (Figs. 14A, 17, 20A). It lacks only in *Euborellia* (Dermaptera) and all representatives of the Caelifera.

49 characteristics of Idvm6 (M. pronoto-cervicalis medialis): (0) single; (1) duplicated

When present, the muscle Idvm6 appears as a single muscle in the majority of investigated taxa (Figs. 16A, 19A, 21A). Only *Zorotypus* (Zoraptera) (Friedrich & Beutel 2008) and the ensiferan *Prosopogryllacris* (Gryllacrididae) are characterized by a two-bundled Idvm6. All members of the Caelifera have a duplicated Idvm6 (Fig. 23B, Supplementary Table 1).

50 Idvm9 (M. profurca-occipitalis): (0) absent; (1) present

Absent in the majority of Polyneoptera and *Siphlonurus* (Ephemeroptera). Present in *Macroxyela* (Hymenoptera), *Tetraphalerus* (Archostemata) and some representatives of the Ensifera (Fig. 21A).

51 Idvm10 (M. profurca-phragmalis): (0) absent; (1) present

Absent in *Palpares* (Neuroptera) and *Siphlonurus* (Ephemeroptera), present in the remaining investigated taxa including all representatives of the Orthoptera (Figs. 16A, 19A, 21A, 23).

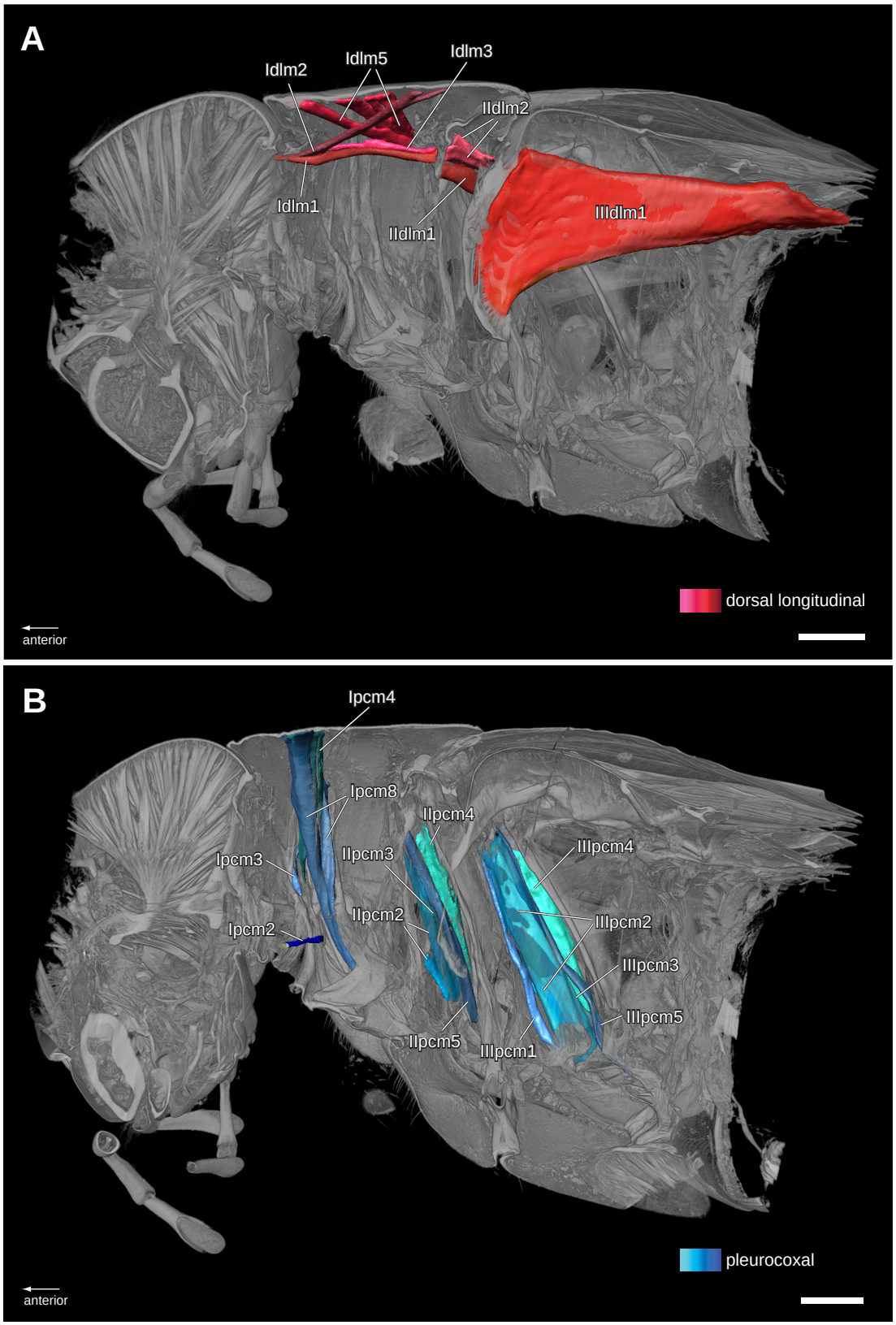


Figure 14. Thoracic muscles of *Gryllus bimaculatus*. Right body half. Interior lateral view. (A) Dorsal longitudinal musculature. (B) Pleurocoxal musulature. Scale bars: 1mm.

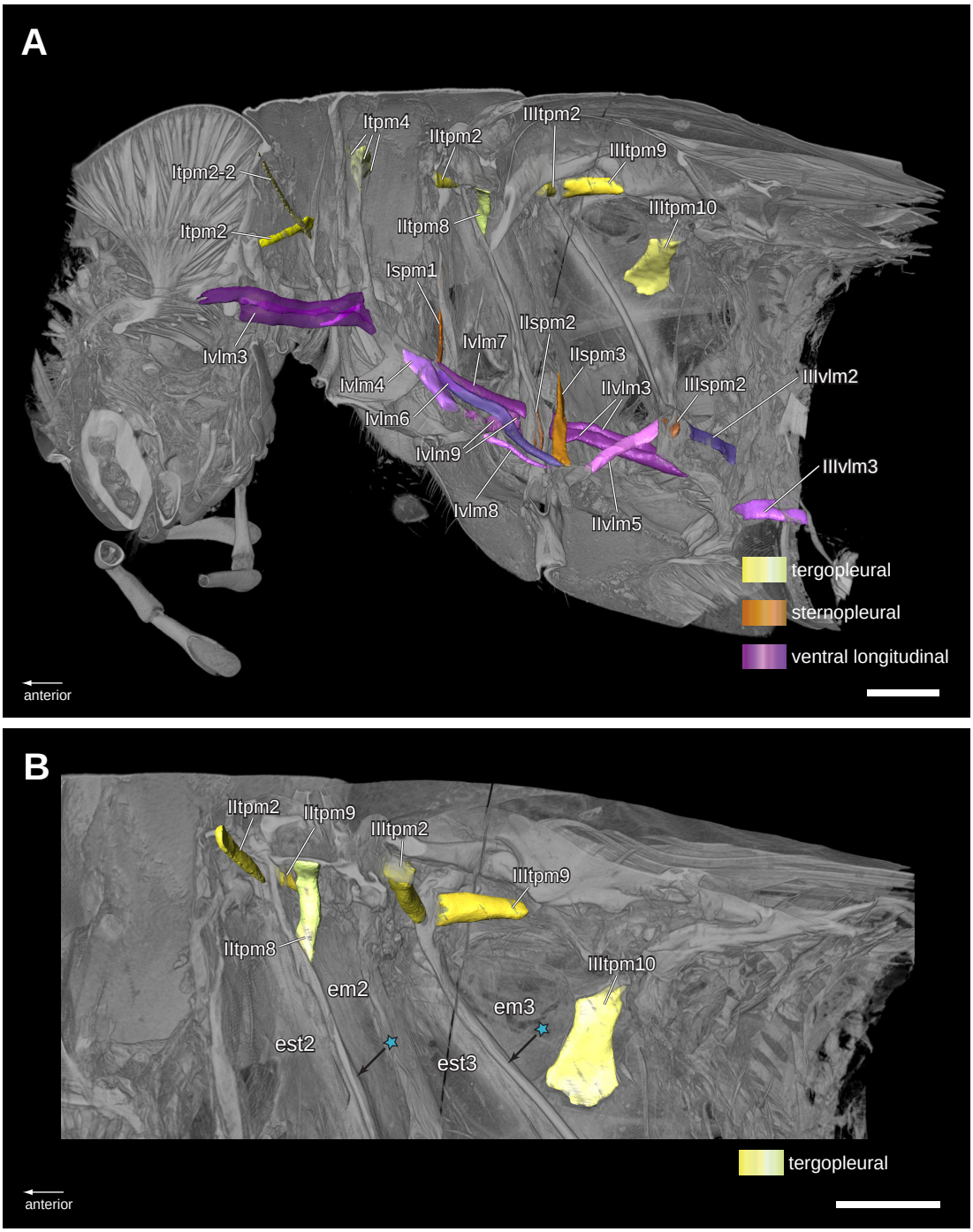
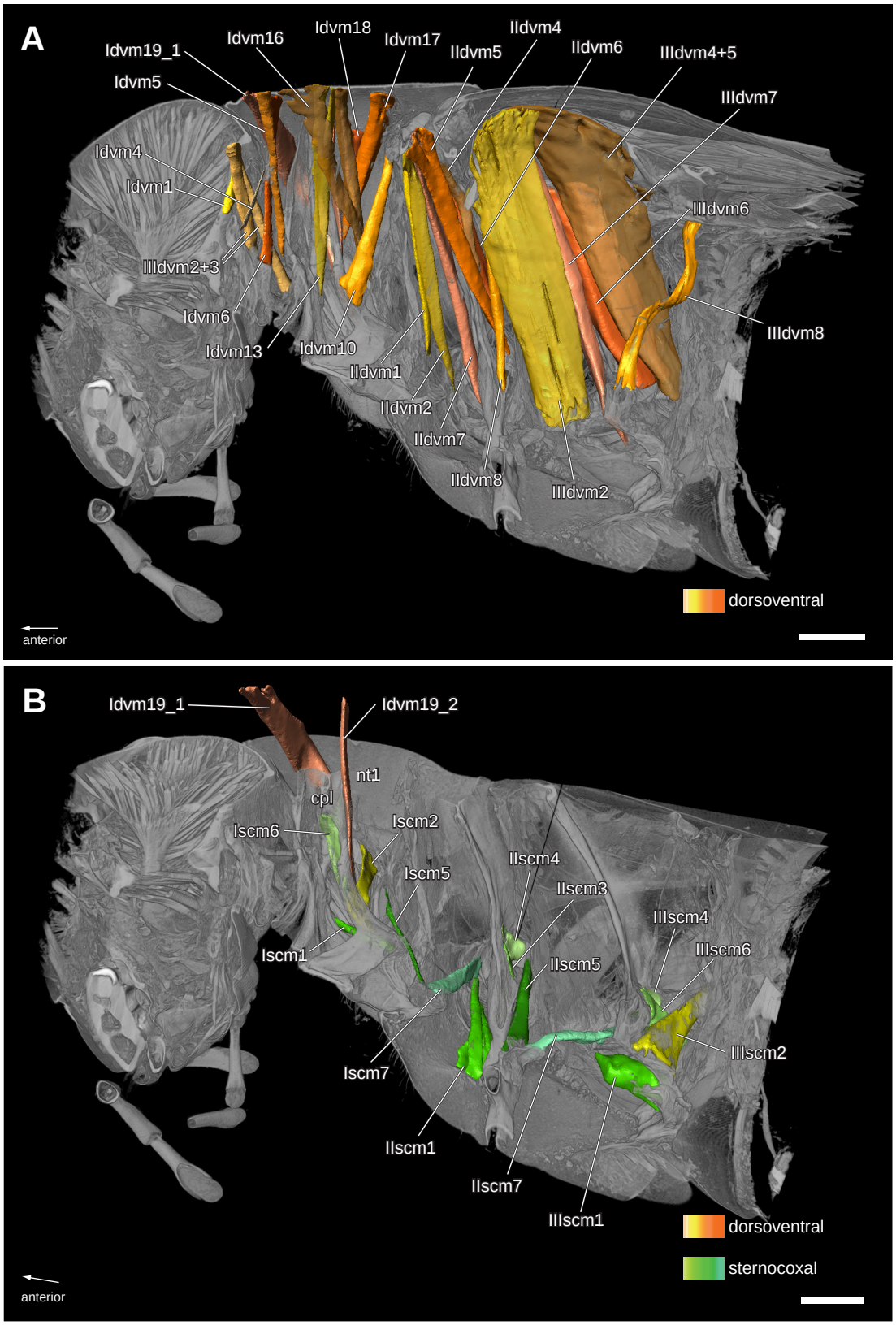


Figure 15. Thoracic muscles of *Gryllus bimaculatus*. Right body half. Interior lateral view. (A) Tergopleural, sternopleural and ventral longitudinal muscles. (B) Slightly shifted dorsolateral view of the pterothorax. Pterothoracic tergopleural muscles. Blue asterisks mark pleural ridge. Abbreviations: *em2/3* meso-/metathoracic epimeron, *est2/3* meso-/metathoracic episternum. Scale bars: 1mm.


A
ldvm19_1
ldvm16
ldvm18
ldvm17
lldvm4
lldvm5
lldvm6
IIIdvm4+5
IIIdvm7
ldvm5
ldvm4
ldvm1
IIIdvm6
IIIdvm2+3
ldvm6
ldvm13
ldvm10
lldvm1
IIIdvm8
lldvm2
lldvm7
lldvm8
IIIdvm2
dorsoventral
anterior
B
ldvm19_1
ldvm19_2
nt1
cpl
lscm6
lscm2
lscm5
lscm1
lscm7
lscm4
lscm3
lscm5
IIIscm4
IIIscm6
IIIscm2
lscm1
lscm7
IIIscm1
dorsoventral
sternocoxal
anterior

52 Idvm12 (M. profurca-mesonotalis): (0) absent; (1) present

Present in *Siphlonurus* (Ephemeroptera), absent in the remaining investigated taxa.

53 Idvm13 (M. pronoto-trochanteralis anterior): (0) absent; (1) present (character 78 of Wipfler *et al.* 2015)

Present in the majority of investigated taxa including all representatives of the Orthoptera (Figs. 16A, 19A, 21A, 23). Absent in *Stenopsocus* (Psocoptera), *Phloeothrips* (Thysanoptera), *Palpares* (Neuroptera) and *Macroxyela* (Hymenoptera).

54 Idvm14 (M. pronoto-trochanteralis anterior): (0) absent; (1) present (character 79 of Wipfler *et al.* 2015)

Present in the majority of Polyneoptera and in *Phloeothrips* (Thysanoptera). Within Polyneoptera, it is absent in *Grylloblatta* (Grylloblattodea), *Euborellia* (Dermaptera) and all representatives of the Orthoptera.

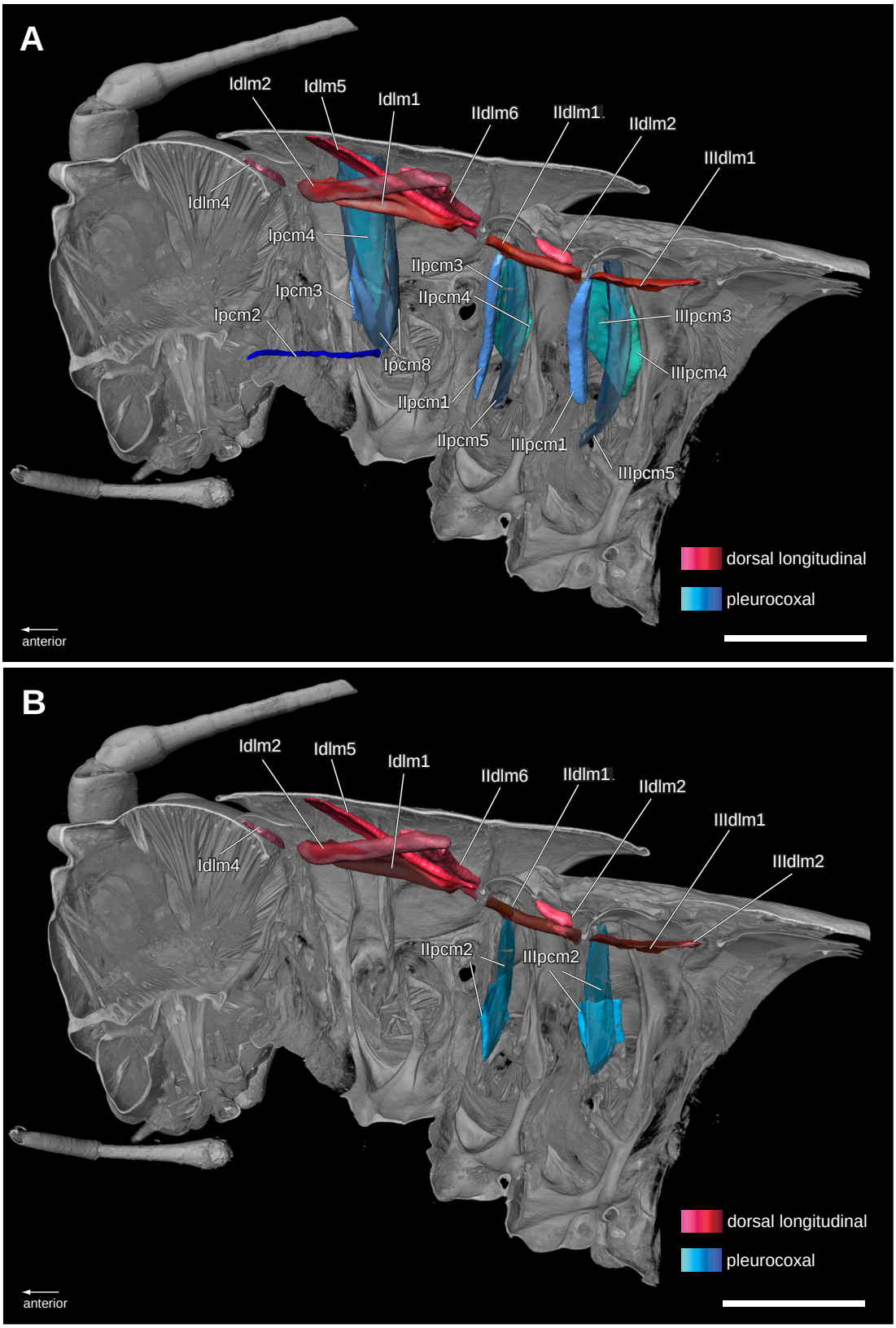
55 Idvm15 (M. pronoto-trochantinocoxalis): (0) absent; (1) present

Present in the majority of Polyneoptera and in *Stenopsocus* (Psocoptera), *Phloeothrips* (Thysanoptera), and *Palpares* (Neuroptera). Absent in *Grylloblatta* (Grylloblattodea) and all representatives of the Orthoptera.

56 characteristics of Idvm19 (M. pronoto-trochanteralis): (0) other; (1) two bundles, the anterior bundle running behind the cryptopleura

When present, the muscle Idvm19 appears as a single muscle in the majority of investigated taxa including the vast majority of Orthoptera (Figs. 19A, 21A, 23B). It is three-bundled in *Zorotypus* (Zoraptera) (two anterior bundles and one posterolateral) and *Stagmomantis* (Mantodea) (all bundles originating from the posterior half of the pronotum). In *Periplaneta* (Blattodea) (different regions of the pronotum), *Gryllotalpa* (Gryllotalpidae) (one bundle from pronotum, the other from cryptopleura), and Gryllidae Idvm19 consists

Figure 16 (see opposite page). Thoracic muscles of *Gryllus bimaculatus*. Right body half. (A) Interior lateral view. Dorsoventral muscles. (B) Interior ventrlateral view. Sternocoxal muscles and Idvm19 (M. pronoto-trochanteralis) Bundle 19_1 runs between the ryptopleura (cpl) and the pronotum (nt1). Scale bars: 1mm.


A
Idlm2
Idlm5
Idlm1
IIdlm6
IIdlm1
IIdlm2
IIIdlm1
Idlm4
Ipcm4
IIpcm3
Ipcm3
IIpcm4
IIIpcm3
Ipcm2
Ipcm8
IIIpcm4
IIpcm1
IIpcm5
IIIpcm1
IIIpcm5
dorsal longitudinal
pleurocoxal
anterior
B
Idlm2
Idlm5
Idlm1
IIdlm6
IIdlm1
IIdlm2
IIIdlm1
IIIdlm2
Idlm4
IIpcm2
IIIpcm2
dorsal longitudinal
pleurocoxal
anterior

of two bundles. The course of the anterior bundle in representatives of the Gryllidae, running anteriorly between the pronotum and cryptopleura (*Gryllus*: Fig. 16B), is unique within Polyneoptera and was considered a possible apomorphy for Gryllidae by Ander (1939).

57 Itpm2 (M. propleuro-occipitalis): (0) absent; (1) present (character 82 of Wipfler *et al.* 2015)

Present in *Siphlonurus* (Ephemeroptera) and some polyneopteran taxa. It is mainly present in Orthoptera (Figs. 18A, 20B, 22B) except *Cephalocoema* (Proscopiidae), Eumastacidae and *Troglophilus* (Rhaphidophoridae).

58 Itpm2-2: (0) absent; (1) present

In Orthoptera, Itpm2 (M. propleuro-occipitalis) runs from the lateral area of the occipital rim to the anterior edge of the cryptopleura (e.g. Fig. 20B). In addition to Itpm2, a further muscle likely having the same function is present in Gryllotalpidae and Gryllidae (*Gryllus*: Fig. 15A). Itpm2-2 is running cross-wise to Itpm2 originating dorsad and inserting ventrad of Itpm2.

59 Itpm3 (M. pronoto-pleuralis anterior): (0) absent; (1) present (character 83 of Wipfler *et al.* 2015)

Present in all investigated taxa except *Phloeothrips* (Thysanoptera) and Orthoptera.

60 Itpm4 (M. pronoto-apodemalis anterior): (0) absent; (1) present

Present in nearly all representatives of the Polyneoptera. Within the Orthoptera, absent in the all taxa except both representatives of the Gryllidae (*Gryllus*: Fig. 15A).

Figure 17 (see opposite page). Thoracic muscles of *Meconema meridionale*. Right body half. Interior lateral view. (A) Dorsal longitudinal and pleurocoxal musculature. (B) Dorsal longitudinal musculature and pterothoracic pcm2 (Mm. basalare-trochantinalis) composed of a long and a short bundle. Scale bars: 1mm.

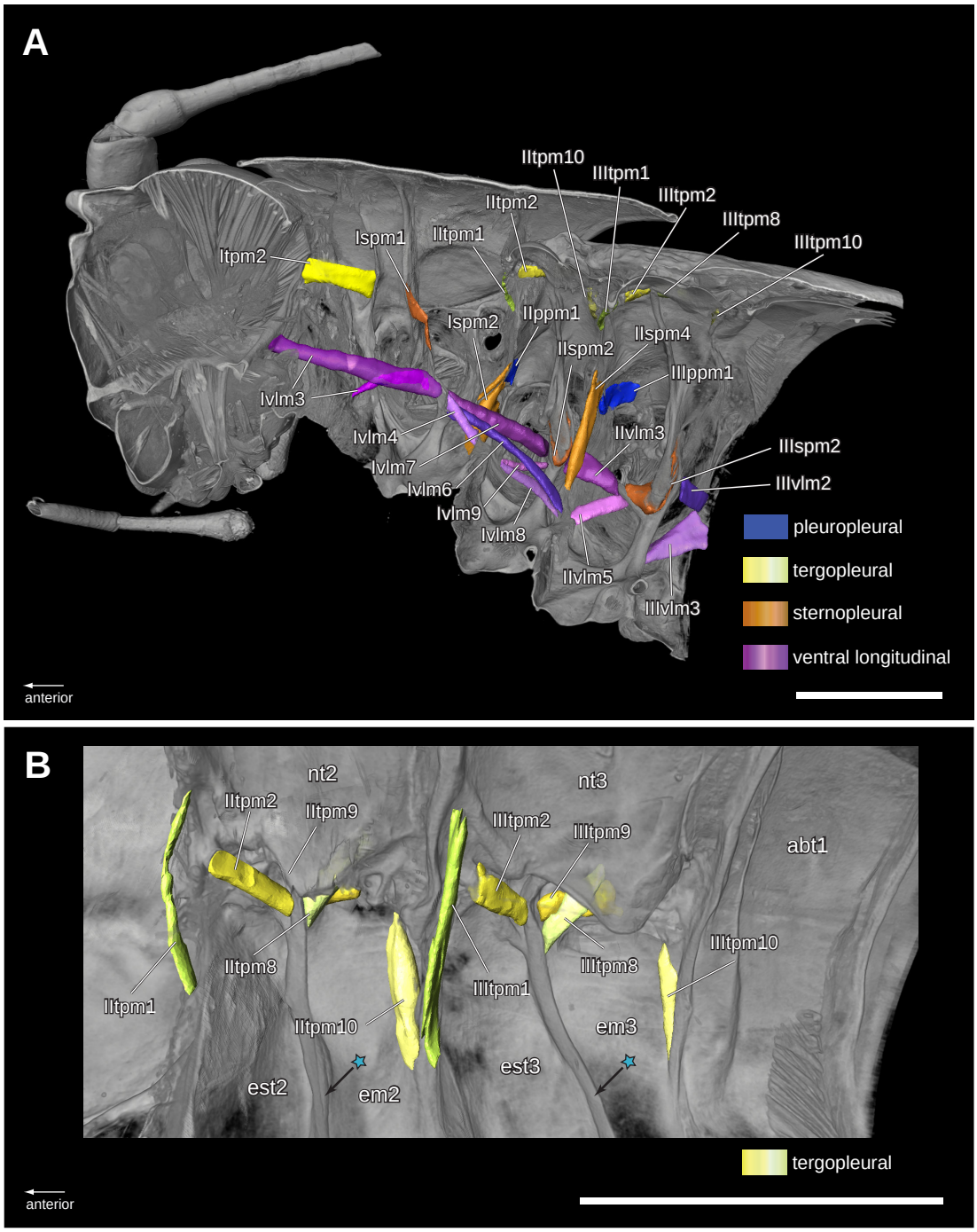


Figure 18. Thoracic muscles of *Meconema meridionale*. Right body half. Interior lateral view. (A) Pleuropleural, tergopleural, sternopleural and ventral longitudinal muscles. (B) Slightly shifted dorsolateral view of the pterothorax. Pterothoracic tergopleural muscles. Blue asterisks mark pleural ridge. Abbreviations: *abt1* first abdominal tergite, *em2/3* meso-/metathoracic epimeron, *est2/3* meso-/metathoracic episternum, *nt2/nt3* meo-/metanotum. Scale bars: 1mm.

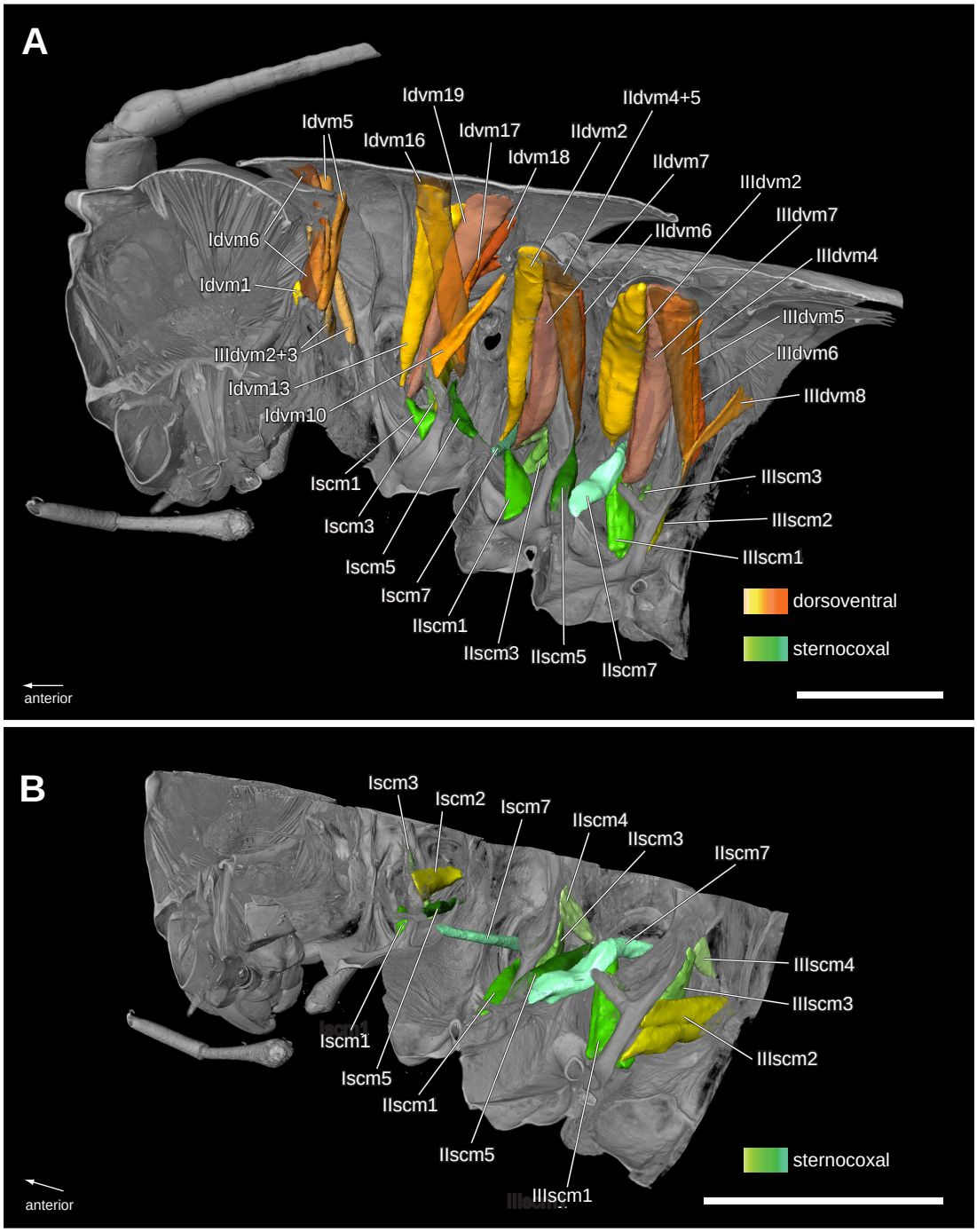
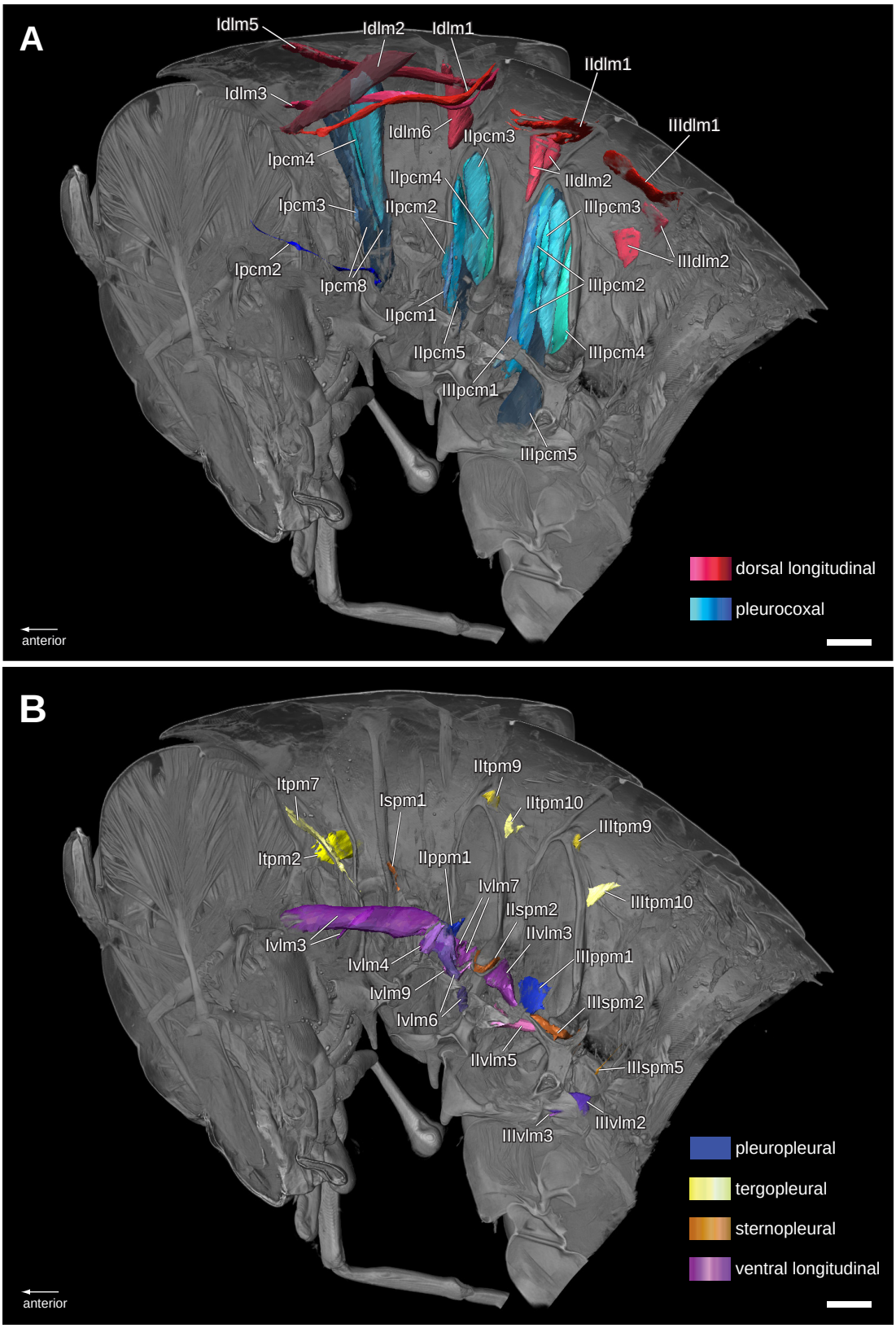


Figure 19. Thoracic muscles of *Meconema meridionale*. Right body half. Interior lateral view. (A) Dorsoventral and sternocoxal muscles. (B) Slightly shifted dorsolateral view, dorsal body half clipped off. Sternocoxal muscles. Scale bars: 1mm.


A
Idlm5
Idlm2
Idlm1
IIdlm1
Idlm3
IIIdlm1
Idlm6
IIpcm3
Ipcm4
IIdlm2
IIpcm4
Ipcm3
IIpcm2
IIIpcm3
IIIdlm2
Ipcm2
Ipcm8
IIIpcm2
IIpcm1
IIpcm5
IIIpcm4
IIIpcm1
IIIpcm5
dorsal longitudinal
pleurocoxal
anterior
B
IItpm9
Itpm7
Ispm1
IItpm10
IIItpm9
Itpm2
IIppm1
Ivlm7
IIIItpm10
IIspm2
Ivlm3
IIvlm3
Ivlm4
IIIppm1
Ivlm9
IIIspm2
Ivlm6
IIvlm5
IIIspm5
IIIvlm2
IIIvlm3
pleuropleural
tergopleural
sternopleural
ventral longitudinal
anterior

61 Itpm7 (M. precoxo-occipitalis): (0) absent; (1) present

Itpm7 is not described in the nomenclature of Friedrich & Beutel (2008). This muscle runs from the dorsal part of the occipital rim, near the originating points of Idlm1 and Idlm2 to the pleurosternal bridge. Itpm7 is only present in both examined representatives of Anostostomatidae, *Hemideina* and *Papuaistus* (Fig. 20B). Its function might be similar to that of Itpm2 and Itm2-2 in stabilizing the large internal cryptopleura.

62 Ispm2 (M. profurca-apodemalis): (0) absent; (1) present (character 86 of Wipfler *et al.* 2015)

This muscle occurs randomly within the taxa investigated. In Orthoptera, this muscle is only present within Ensifera (Figs. 15A, 18A, 20A), although it is absent in some representatives (*Comicus*, *Stenopelmatus*, *Troglophilus*, *Gryllotalpa*).

63 origin of Ispm2 (M. prospina-mesopleuralis): (0) directly on prospina; (1) laterally on spinasternite; (2) laterally on posterior sternal plate

According to Friedrich & Beutel (2008), Ispm2 originates from the prospina and inserts at the mesepisternum, mesobasalare, or ventrolateral area of the prophragma. In *Grylloblatta* (Grylloblattodea), *Austrophasma* (Mantophasmatodea), *Periplaneta* (Blattodea), *Stagmomantis* (Mantodea), and *Zorotypus* (Zoraptera) the muscle originates directly from the prospina. Within Ensifera, Ispm2 is only present in Tettigoniidae and originates laterally from the spinasternite (Fig. 18A). In Phasmatodea, *Timema* and *Megacrania*, Ispm2 originates laterally on the posterior sternal plate. Since the homology of the posterior sternal plate in the thorax of Phasmatodea is questionable (Jeziorski 1918; Matsuda 1970), this character is coded as an independent character state for these taxa.

64 Ispm3 (M. prospina-intersegmentalis): (0) absent; (1) present (character 87 of Wipfler *et al.* 2015)

Only present in *Euborellia* (Dermaptera) and *Zorotypus* (Zoraptera).

Figure 20. Thoracic muscles of *Papuaistus* sp. Right body half. Interior lateral view. (A) Dorsal longitudinal and pleurocoxal muscles. (B) Pleuropleural, tergopleural, sternopleural and ventral longitudinal musles. IIspm3 not illustrated. Scale bars: 1mm.

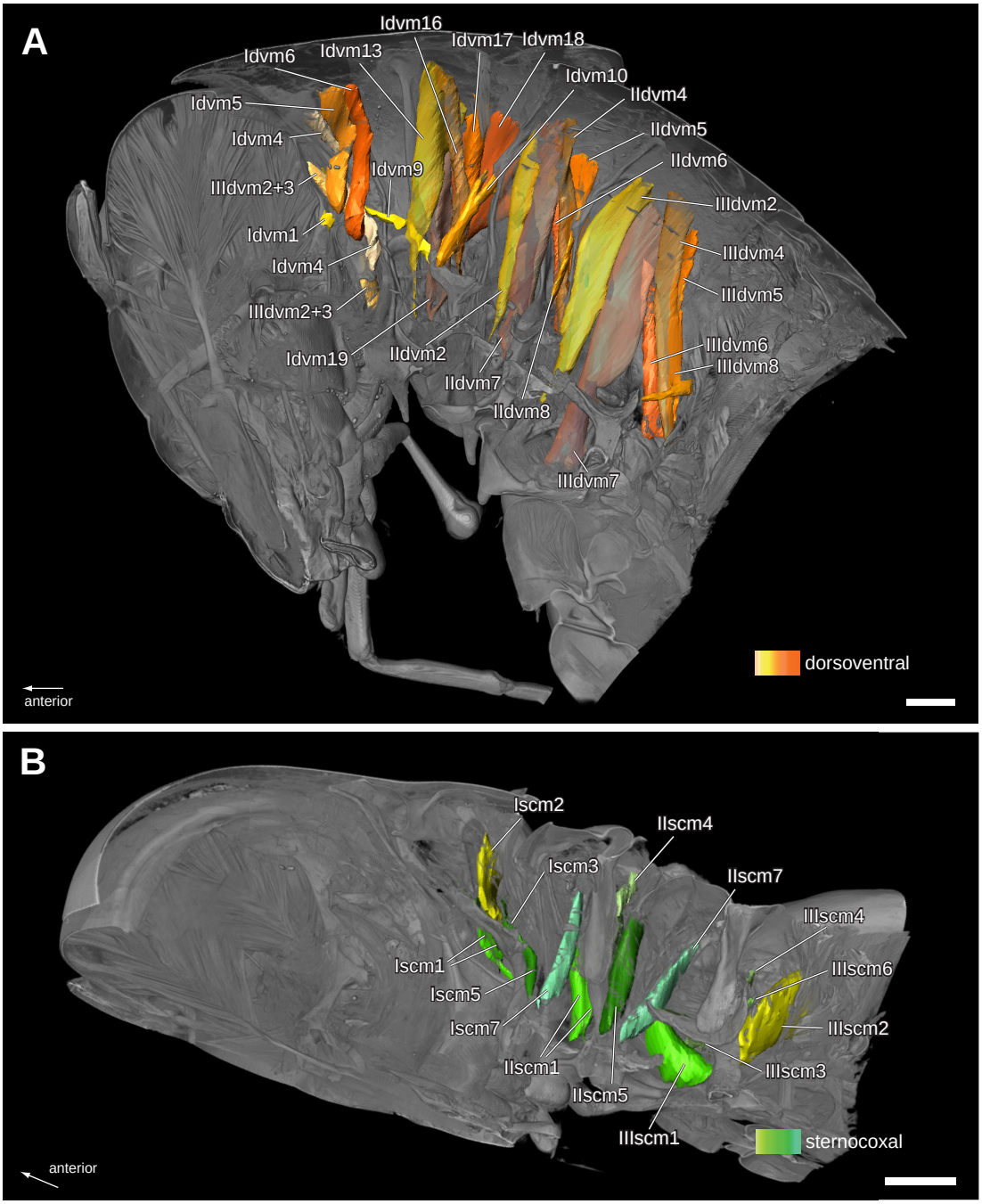


Figure 21. Thoracic muscles of *Papuaistus* sp. Right body half. (A) Interior lateral view. Dorsventral muscles. (B) Slightly shifted ventrolateral view, dorsal body half clipped off. Sternocoxal musles. Scale bars: 1mm.

65 Ipcm2 (M. procoxa-cervicalis transversalis): (0) absent; (1) present (character 88 of Wipfler *et al.* 2015)

Absent in the majority of taxa. It is present in *Grylloblatta* (Grylloblattodea) *Stenopsocus* (Psocoptera) and *Macroxyela* (Hymenoptera). Within the Ensifera, this muscle is present

in the majority of taxa (Figs. 14B, 17A, 20A), although it is absent in some representatives (*Comicus*, *Stenopelmatus*, *Prosopogryllacris* and *Gryllotalpa*). Within the investigated caeliferan representatives, this muscle is only present in *Xya* (Tridactylidae).

66 Ipcm3 (M. propleuro-trochantinalis): (0) absent; (1) present

Absent in the majority of investigated taxa, present in *Megacrania* (Phasmatodea) and all representatives of the Ensifera (Figs. 14B, 17A, 20A) except *Gryllotalpa*.

67 Ivlm6 (M. profurca-mesospinalis): (0) absent; (1) present (character 91 of Wipfler *et al.* 2015)

This muscle occurs randomly within the taxa investigated. Regarding the Orthoptera, it is only present in the representatives of the Ensifera (Figs. 15A, 18A, 20B).

68 Ivlm8 (M. prospina-mesospinalis): (0) absent; (1) present (character 92 of Wipfler *et al.* 2015)

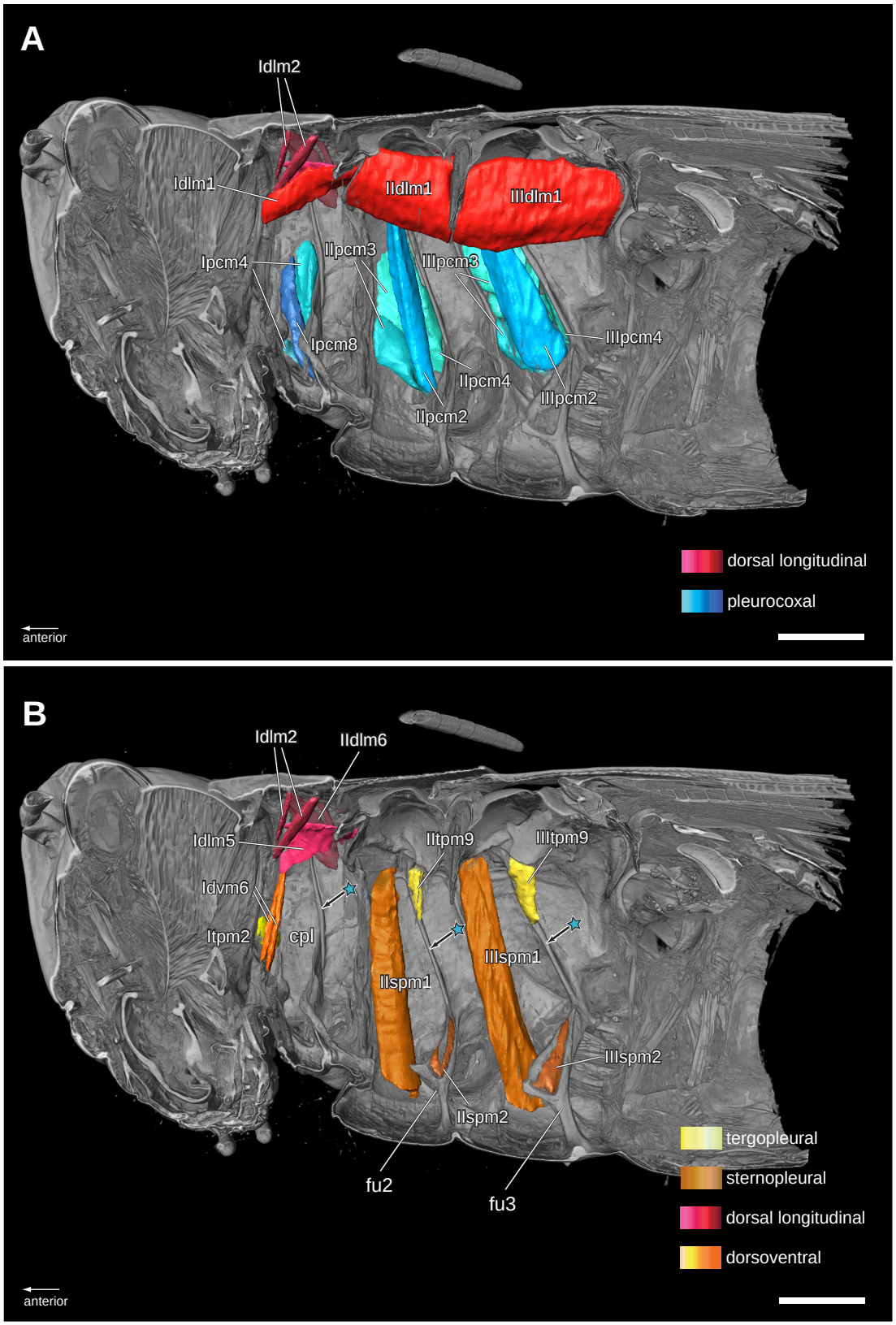
Present in *Stenopsocus* (Psocoptera), *Periplaneta* (Blattodea), and *Stagmomantis* (Mantodea). It is also present in the vast majority of Orthoptera (Figs. 15A, 18A, 24A) except *Comicus* and *Papuaistus*.

69 characteristics of Ivlm8: (0) paired; (1) unpaired

Following the bilateral symmetric scheme, each thoracic muscle is paired as it is present in both body halves. If present, the muscle Ivlm8 is paired in the taxa investigated. To the contrary, Ivlm8 is unpaired in *Gryllus*, *Acheta* and *Gryllotalpa* (Voss 1905c; La Greca 1938).

70 Ivlm10 (M. profurca-cervicalis transversalis): (0) absent; (1) present

Ivlm10 is not described in the nomenclature of Friedrich & Beutel (2008). It originates from the profurca and runs transversally to the posterior edge of the first cervical sclerite of the opposite body side. This muscle is only present in all representatives of the Caelifera (Fig. 24A) except *Xya*.


A
Idlm2
Idlm1
IIdlm1
IIIdlm1
Ipcm4
IIpcm3
IIIpcm3
IIIpcm4
Ipcm8
IIpcm4
IIIpcm2
IIpcm2
dorsal longitudinal
pleurocoxal
anterior
B
Idlm2
IIdlm6
Idlm5
IItpm9
IIItpm9
Idvm6
Itpm2
cpl
IIIspm1
IIspm1
IIIspm2
IIspm2
fu2
fu3
tergopleural
sternopleural
dorsal longitudinal
dorsoventral
anterior

71 Iscm2 (M. profurca-coxalis posterior): (0) absent; (1) present (character 93 of Wipfler *et al.* 2015)

The muscle occurs randomly within the taxa investigated. Regarding the Orthoptera, this muscle is only present in Ensifera (Figs. 16B, 19B, 21B), whereas it is absent in all investigated taxa of the Caelifera.

Mesothorax

72 characteristics of IIdvm1 (M. mesonoto-sternalis): (0) single; (1) multiplicated

When present, IIdvm1 appears as a single muscle in the majority of Polyneoptera (Fig. 16A). In contrast, the winged morph of *Zorotypus* (Zoraptera) (Friedrich & Beutel 2008) and some representatives of the Caelifera, namely the grasshoppers *Dissosteira*, *Locusta*, *Schistocerca* and *Stenobothrus* (Acrididae) are characterized by a multiplicated IIdvm1 (Fig. 23A).

73 IIdvm2 (M. mesonoto-trochantinalis anterior): (0) absent; (1) present (character 97 of Wipfler *et al.* 2015)

Generally present in Polyneoptera (Figs. 16A, 19A, 21A, 23B) with the exception of *Timema* (Phasmatodea) and *Comicus* (Schizodactylidae). It is absent in *Stenopsocus* (Psocoptera), *Phloeothrips* (Thysanoptera), *Palpares* (Neuroptera), and *Tetraphalerus* (Archostemata).

74 IIdvm8 (M. mesofurca-phragmalis): (0) absent; (1) present

Whereas this muscle is present in Polyneoptera (except the mantophasmatodean *Austrophasma*), it is merely present in some representatives of Orthoptera (Figs. 16A, 21A).

75 IIdvm9 (M. mesospina-phragmalis): (0) absent; (1) present (character 99 of Wipfler *et al.* 2015)

Only present in *Timema* and *Megacrania*, both being representatives of the Phasmatodea.

Figure 22 (see opposite page). Thoracic muscles of *Stenobothrus lineatus*. Right body half. Interior lateral view. (A) Dorsal longitudinal and pleurocoxal muscles. (B) Tergopleural and sernopleural musles, selected dorsal longitudinal and dorsoventral muscles. Scale bars: 1mm.

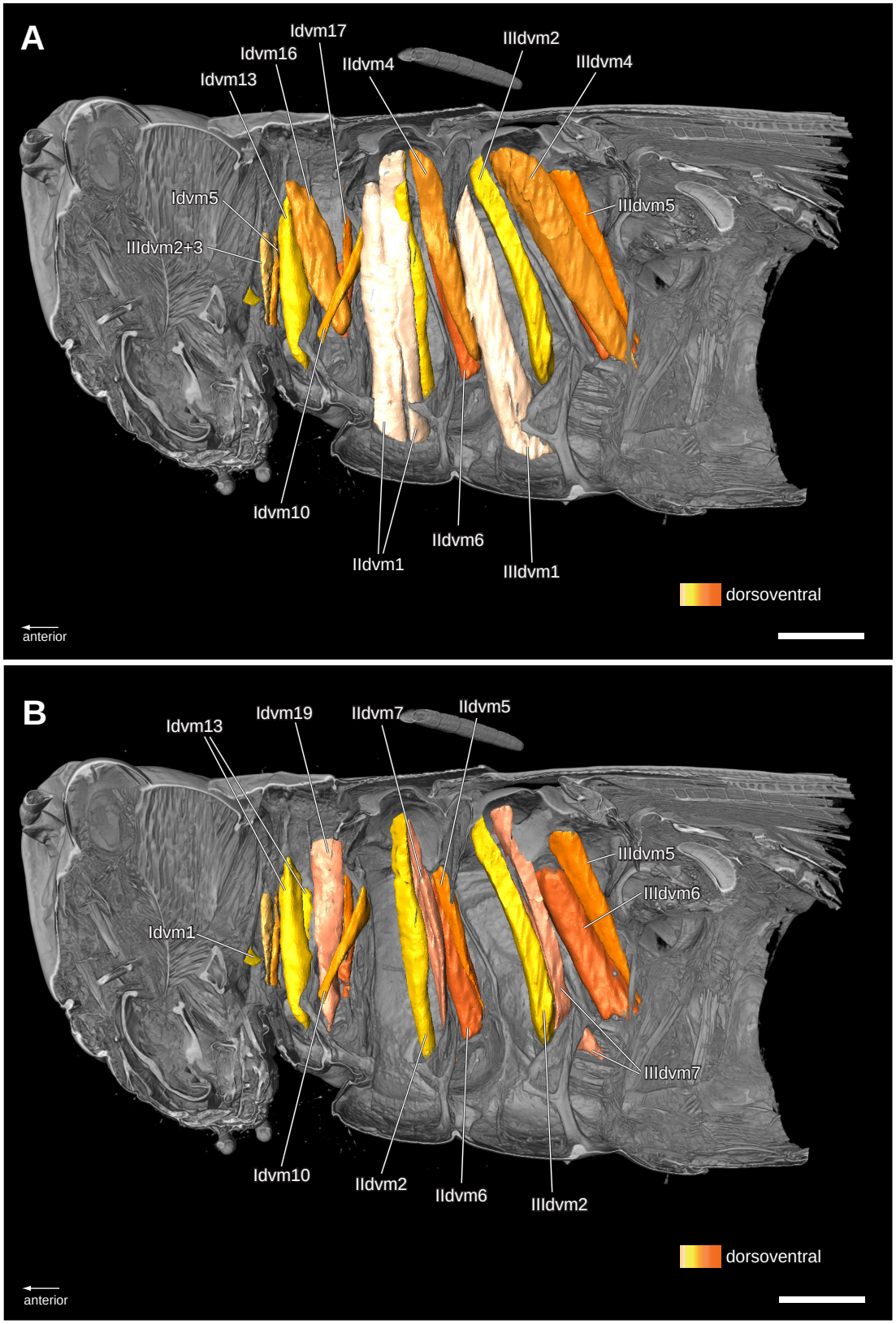


Figure 23. Thoracic muscles of *Stenobothrus lineatus*. Right body half. Interior lateral view. Dorsaoventral muscles. (A), (B) Virtual dissection. Scale bars: 1mm.

76 IItpm6 (M. mesonoto-pleuralis posterior): (0) absent; (1) present

Absent in all representatives of Orthoptera. Within Polyneoptera, IItpm6 is present in *Megacrania* (Phasmatodea), *Periplaneta* (Blattodea), *Stagmomantis* (Mantodea), *Perla* (Plecoptera), and *Zorotypus* (Zoraptera). This muscle is also present in the holometabolans *Palpares* (Neuroptera) and *Tetraphalerus* (Archostemata).

77 IItpm7 (M. mesanepisternalis-axillaris): (0) absent; (1) present

Absent in all representatives of Orthoptera. Within Polyneoptera, IItpm7 is only present in *Embia* (Embioptera), *Perla* (Plecoptera) and the winged morph of *Zorotypus* (Zoraptera). Also present in the holometabolans *Palpares* (Neuroptera) and *Tetraphalerus* (Archostemata).

78 pterothoracic tpm13 (M. mesonoto-episternalis): (0) absent; (1) present

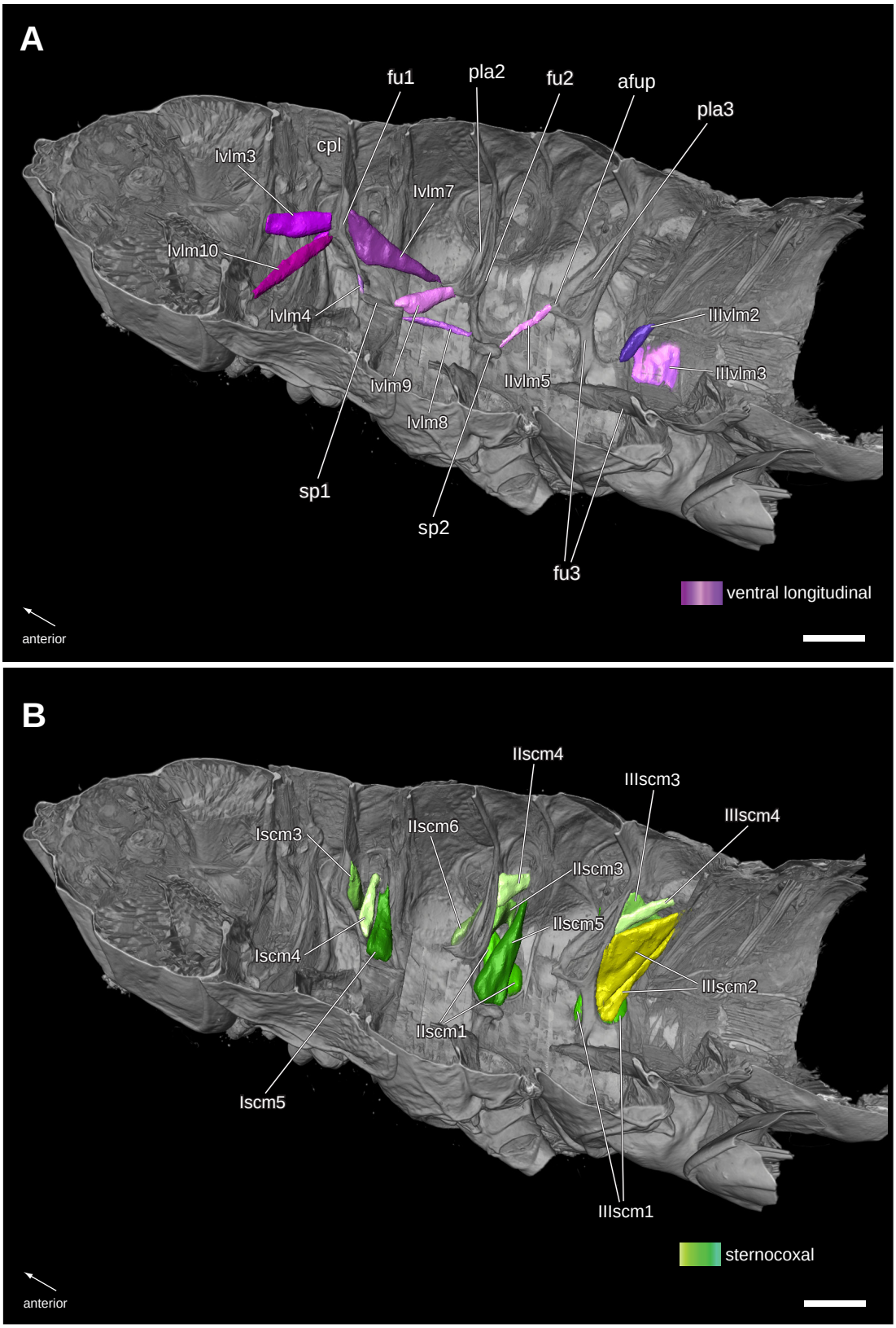
Muscle tpm13 (present in meso-and metathorax) is not described in the nomenclature of Friedrich & Beutel (2008). Its definition and designation follows the study of Klug (2008). This muscle is a unique feature of Phasmatodea. It occurs simultaneously in both pterothoracic segments of the phasmatodean thorax. Since the presence of these muscles is not independent from each otherthe presence or absence of this muscle in the meso-and metathoracic segment is treated as a single character.

79 IIppm1 (M. mesotransanapleuralis): (0) absent; (1) present

Present in *Perla* (Plecoptera), *Megacrania* (Phasmatodea), *Palpares* (Neuroptera), and all representatives of the Ensifera (Figs. 18A, 20B).

80 IIspm3 (M. mesospina-metanepisternalis): (0) absent; (1) present (character 101 of Wipfler *et al.* 2015)

Present in a wide range of Polyneoptera. In Orthoptera, this muscle occurs only within Ensifera (Figs. 15A, 18A) with the exception of *Comicus* (Schizodactylidae) and *Troglophilus* (Rhaphidophoridae).


A
fu1
pla2
fu2
afup
pla3
cpl
lvlm3
lvlm7
lvlm10
lvlm4
IIIvlm2
IIIvlm3
lvlm9
IIvlm5
lvlm8
sp1
sp2
fu3
ventral longitudinal
anterior
B
IIscm4
IIIscm3
IIIscm4
lscm3
IIscm6
IIscm3
IIscm5
lscm4
IIIscm2
IIscm1
lscm5
IIIscm1
sternocoxal
anterior

81 IIpcm1 (M. mesanepisterno-trochantinalis): (0) absent; (1) present (character 103 of Wipfler *et al.* 2015)

Present in *Periplaneta* (Blattodea), *Stagmomantis* (Mantodea), *Euborellia* (Dermaptera), *Megacrania* (Phasmatodea), *Stenopsocus* (Psocoptera), and *Phloeothrips* (Thysanoptera). Regarding the Orthoptera, this muscle is solely present in Ensifera (Figs. 14B, 17A, 20A).

82 IIpcm5 (M. mesanepisterno-trochanteralis): (0) absent; (1) present (character 106 of Wipfler *et al.* 2015)

Present in the vast majority of investigated taxa, absent in *Phloeothrips* (Thysanoptera) and *Palpares* (Neuroptera). In Orthoptera, this muscle occurs only in Ensifera (Figs. 14B, 17A, 20A), whereas it is absent in Caelifera.

83 IIpcm6 (M. mesopleura-trochanteralis): (0) absent; (1) present

Present only in the holometabolans *Palpares* (Neuroptera) and *Tetraphalerus* (Coleoptera: Archostemata).

84 IIvlm3 (M. mesofurca-metafurcalis): (0) absent; (1) present

Present in the vast majority of investigated taxa (Figs. 15A, 18A, 20B). It is absent in *Siphlonurus* (Ephemeroptera), *Megacrania* (Phasmatodea) and the caeliferan representatives *Cephalocoema* (Proscopiidae) and Eumastacidae.

85 characteristics of IIvlm3: (0) distinct muscle; (1) sclerotized fiber

When present, IIvlm3 appears as a distinct muscle with contractile muscle fibers in the majority of investigated taxa. Only within the Caelifera, in *Stenobothrus*, *Schistocerca*, *Locusta*, and *Dissosteira*, the respective muscle is merely a sclerotized fiber connecting the mesofurca and the metafurca (Snodgrass 1929; Misra 1947; Albrecht 1953).

Figure 24 (see opposite page). Thoracic muscles of *Stenobothrus lineatus*. Right body half. Slightly shifted ventrolateral view, dorsal body half cut off. (A) Ventrl longitudinal muscles. (B) Sternocoxal muscles. Abbreviations: *afup* anterior metafural process, *cpl* cryptopleura, *fu1/2/3* pro-/meso-/metafura, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.

86 IIscm2 (M. mesofurca-coxalis posterior): (0) absent; (1) present

Present in the vast majority of investigated taxa. The muscle is absent only in *Grylloblatta* (Grylloblattodea), *Austrophasma* (Mantophasmatodea) and in all representatives of the Orthoptera.

87 IIscm3 (M. mesofurca-coxalis medialis): (0) absent; (1) present (character 107 of Wipfler *et al.* 2015)

Present in all representatives of Orthoptera and the majority of the remaining Polyneoptera (Figs. 16B, 19, 21B, 24B). The muscle is absent in *Euborellia* (Dermaptera), *Stagmomantis* (Mantodea), and *Periplaneta* (Blattodea). Also absent in *Siphlonurus* (Ephemeroptera), and all representatives of the Eumetabola, *Stenopsocus* (Psocoptera), *Phloeothrips* (Thysanoptera), *Palpares* (Neuroptera), and *Tetraphalerus* (Coleoptera: Archostemata).

88 IIscm4 (M. mesofurca-coxalis lateralis): (0) absent; (1) present (character 108 of Wipfler *et al.* 2015)

Present in the vast majority of investigated taxa including all representatives of the Orthoptera (Figs. 16B, 19B, 21B, 24B), absent only in *Periplaneta* (Blattodea), *Timema* and *Megacrania* (Phasmatodea), and *Palpares* (Neuroptera).

89 IIscm5 (M. mesospina-coxalis): (0) absent; (1) present (character 109 of Wipfler *et al.* 2015)

The muscle occurs randomly within the taxa investigated. In Orthoptera, this muscle is commonly present (Figs. 16B, 19, 21B, 24B).

90 IIscm6 (M. mesofurca-trochanteralis): (0) absent; (1) present (character 110 of Wipfler *et al.* 2015)

Present in the vast majority of investigated taxa including all representatives of the Orthoptera (Figs. 16B, 19, 21B, 24B). This muscle is absent in *Siphlonurus* (Ephemeroptera), *Grylloblatta* (Grylloblattodea), and both representatives of the Phasmatodea.

91 IIscm7 (M. mesospina-metacoxalis): (0) absent; (1) present (character 111 of Wipfler *et al.* 2015)

The muscle occurs randomly within the taxa investigated. Regarding the Orthoptera, this muscle is only present in Ensifera (Figs. 16B, 19, 21B).

Metathorax

92 IIIdvm1 (M. metanoto-sternalis): (0) absent; (1) present

Absent in a wide range of investigated taxa. Within the Orthoptera, this muscle is only present in *Schistocerca*, *Dissosteira*, *Locusta*, and *Stenobothrus* (Fig. 23A).

93 IIIdvm3 (M. metanoto-trochantinalis posterior): (0) absent; (1) present (character 112 of Wipfler *et al.* 2015)

Present in the majority of Polyneoptera. This muscle is absent in *Perla* (Plecoptera), *Grylloblatta* (Grylloblattodea) and all representatives of the Orthoptera. Also absent in *Stenopsocus* (Psocoptera), *Phloeoethrips* (Thysanoptera), *Macroxyela* (Hymenoptera) and *Tetraphalerus* (Coleoptera: Archostemata).

94 IIIppm1 (M. metatransanapleuralis): (0) absent; (1) present

The muscle is rarely present in Polyneoptera, as it occurs only in *Perla* (Plecoptera), *Megacrania* (Phasmatodea), and some representatives of the Ensifera (Figs. 18A, 20B). It is also present in the holometabolans *Palpares* (Neuroptera) and *Tetraphalerus* (Coleoptera: Archostemata).

95 IIIspm5 (M. metafurca-intersegmentalis posterior): (0) absent; (1) present

Only present in *Austrophasma* (Mantophasmatodea) and some representatives of the Ensifera (Fig. 20B).

96 IIIpcm1 (M. metaanepisterno-trochantinalis): (0) absent; (1) present (character 113 of Wipfler *et al.* 2015)

The muscle occurs randomly within the taxa investigated. Regarding the Orthoptera, this muscle is only present in the representatives of the Ensifera (Figs. 14B, 17A, 20A).

97 IIIpcm5 (M. metanepisterno-trochanteralis): (0) absent; (1) present

Present in the majority of investigated taxa including all representatives of the Ensifera (Figs. 14B, 17A, 20A). This muscle is absent in *Megacrania* (Phasmatodea), all representatives of the Caelifera, and the holometabolans *Palpares* (Neuroptera), *Macroxyela* (Hymenoptera), and *Tetraphalerus* (Coleoptera: Archostemata).

98 IIIvlm1 (M. metafurca-spinalis): (0) absent; (1) present

Only present in *Siphlonurus* (Ephemeroptera), *Megacrania* (Phasmatodea) and the caeliferans *Xya* (Tridactylidae) and Eumastacidae (Blackith & Blackith 1967).

99 IIIscm2 (M. metafurca-coxalis posterior): (0) absent; (1) present (character 116 of Wipfler *et al.* 2015)

Present in the vast majority of investigated taxa including all representatives of the Orthoptera (Figs. 16B, 19, 21B, 24B). This muscle is absent in *Grylloblatta* (Grylloblattodea) and *Austrophasma* (Mantophasmatodea).

100 IIIscm3 (M. metafurca-coxalis medialis): (0) absent; (1) present (character 117 of Wipfler *et al.* 2015)

Present in Polyneoptera including all representatives of the Orthoptera (Fig. 16B, 19, 21B, 24B). It is absent in *Stenopsocus* (Psocoptera), *Phloeothrips* (Thysanoptera), *Palpares* (Neuroptera), *Macroxyela* (Hymenoptera), and *Tetraphalerus* (Coleoptera: Archostemata).

101 IIIscm4 (M. metafurca-coxalis lateralis): (0) absent; (1) present (character 118 of Wipfler *et al.* 2015)

The muscle is present in all representatives of the Orthoptera (Fig. 16B, 19, 21B, 24B). It is absent in *Perla* (Plecoptera), both representatives of the Phasmatodea, *Stenopsocus* (Psocoptera), and *Palpares* (Neuroptera).

102 IIIscm5 (M. metaspina-coxalis): (0) absent; (1) present (character 119 of Wipfler *et al.* 2015)

Only present in *Austrophasma* (Mantophasmatodea) and *Grylloblatta* (Grylloblattodea).

Characters of the wing and wing base

The characters of the wing and wing base were adopted from Yoshizawa (2011) and Beutel & Gorb (2001, 2006). Character coding was adopted from Wipfler *et al.* (2015). As this character complex was not examined for all orthopteran representatives herein studied, the character states for the enlarged sampling were also adopted from previous studies that proposed a certain character state for Ensifera and Caelifera respectively (Yoshizawa 2011; Wipfler *et al.* 2015).

103 Wings: (0) absent; (1) present (character 32 of Wipfler *et al.* 2015)

Secondary winglessness is common among the investigated species. In Caelifera, the representatives *Cephalocoema* (Proscopiidae) and Eumastacidae are wingless. Within the Ensifera, wings lack in *Comicus* (Schizodactylidae), in *Papuaistus* and *Hemideina* (Anostostomatidae), in *Stenopelmatus* (Stenopelmatidae), and in *Troglophilus* (Rhaphidophoridae). All following characters depending on the wing anatomy and wing base structures in particular were coded as "not applicable" for wingless taxa.

104 Costal cross veins: (0) more than 5; (1) less than 5 (character 33 of Wipfler *et al.* 2015, character 46 of Beutel & Gorb 2001)

After Beutel & Gorb (2001), the presence of more than five cross veins meeting the anterior margin of the hind wing is a characteristic of some basal lineages of Pterygota and of the neuropteroid orders.

105 Hind wing vannus: (0) not enlarged; (1) distinctly enlarged (character 34 of Wipfler *et al.* 2015, character 47 of Beutel & Gorb 2001)

The vannus is the area of the neopteran wing that contains the anal veins (Snodgrass 1935). A distinctly enlarged hind wing vannus was considered a possible apomorphy of the lower neopteran orders by Kristensen (1991).

106 Folding of vannus: (0) few anal veins, not pleated; (1) pleated (character 35 of Wipfler *et al.* 2015, character 48 of Beutel & Gorb 2001)

After Kristensen (1981), a pleated hind wing vannus represents a potential synapomorphy

of Phasmatodea, Orthoptera, Dermaptera, Grylloblattodea, Zoraptera, and Dictyoptera (his Orthopterodida).

107 Sclerotization of forewing: (0) absent; (1) moderately sclerotized tegmina; (2) strongly shortened sclerotized tegmina; (3) elytra (character 36 of Wipfler *et al.* 2015, character 50 of Beutel & Gorb 2001)

The sclerotization of the forewings in lower Neoptera is assumed to represent a gradual transformation from membranous forewings into sclerotized tegmina (Beutel & Gorb 2001).

108 Pronounced precostal field: (0) absent; (1) present (character 37 of Wipfler *et al.* 2015, character 52 of Beutel & Gorb 2001)

Wings with a distinct precostal field are only present in the Orthoptera and Phasmatodea investigated. This character was previously thought to represent a potential apomorphy of Phasmatodea and Orthoptera (Kristensen 1981).

109 Folding lines: (0) basal hinge only; (1) with additional folding lines (character 38 of Wipfler *et al.* 2015, character 43 of Beutel & Gorb 2001, character 1 of Yoshizawa 2011)

Folding lines at the wing base and a characteristic arrangement of axillary sclerites enable neopterans to fold back their wings over the abdomen (Snodgrass 1935). Yoshizawa (2011) confirms this character to represent an unambiguous apomorphy of Neoptera.

110 Antemedian notal wing process: (0) not clearly differentiated; (1) well developed (character 39 of Wipfler *et al.* 2015, character 2 of Yoshizawa 2011)

The antemedian notal wing prosess is situated between the median notal wing process and the anterior notal wing process, usually closer to the latter one. It is not clearly developed in the representatives of the Holometabola, Psocoptera, Phasmatodea, Zoraptera and Ephemeroptera investigated (Willkommen 2008; Yoshizawa 2011).

111 Median notal wing process: (0) separated from notum; (1) fused to notum; (2) absent (character 40 of Wipfler *et al.* 2015, character 3 of Yoshizawa 2011)

A median notal wing process that is fused to the notum is found in the majority of investigated taxa. Yoshizawa (2011) found this character state to be an unambiguous apomorphy for Neoptera, whereby he includes Polyneoptera, alderflies (Megaloptera), scorpionflies (Mecoptera), and lice (Psocodea) in his analysis.

112 Posterior notal wing process: (0) separated from notum; (1) fused to notum (character 41 of Wipfler *et al.* 2015, character 4 of Yoshizawa 2011)

A posterior notal wing process that is fused to the notum is found in the Dictyoptera, Dermaptera, Plecoptera and Embioptera as well as in Phasmatodea, Psocoptera and Thysanoptera that were investigated herein (Yoshizawa & Saigusa 2001; Willkommen & Hörnschemeyer 2007; Yoshizawa 2011).

113 Tegula: (0) membranous or less developed; (1) strongly sclerotized (character 42 of Wipfler *et al.* 2015)

The tegula, a large scale-like lobe that overlaps the base of the forewing (Snodgrass 1935), is sclerotized in Embioptera and Zoraptera. This was found an unambiguous apomorphic character of both taxa (= Mystroptera) in the analysis of Yoshizawa (2011).

114 Humeral plate, ventral: (0) not sclerotized; (1) sclerotized (character 43 of Wipfler *et al.* 2015, character 6 of Yoshizawa 2011)

The humeral plate is an anterior preaxillary sclerite in the wing base that supports the costal vein (Snodgrass 1935). Its ventral part is sclerotized in the majority of examined taxa. Yoshizawa (2011) found this character state to be an unambiguous apomorphy for Neoptera, whereby he includes Polyneoptera, alderflies (Megaloptera), scorpionflies (Mecoptera), and lice (Psocodea) in his analysis.

115 Humeral plate, dorsal: (0) sclerotized; (1) membranous (character 44 of Wipfler *et al.* 2015, character 7 of Yoshizawa 2011)

After Yoshizawa (2011), the dorsal part of the humeral plate is sclerotized in the plesiomorphic condition of Pterygota. He found the character change from sclerotized to membranous to be an unambiguous apomorphy of Polyneoptera (Yoshizawa 2011).

116 Humeral plate and ventral basisubcostale: (0) widely separated; (1) closely associated; (2) fused (character 45 of Wipfler *et al.* 2015, character 8 of Yoshizawa 2011)

In Dictyoptera, Psocoptera and Hymenoptera the humeral plate is fused ventrally to the basisubcostale. In Dermaptera, Zoraptera, Embioptera and Neuroptera both elements are closely related, whereas they are distinctly separated in the remaining taxa.

117 Humeral plate and dorsal basisubcostale: (0) separated; (1) fused (character 46 of Wipfler *et al.* 2015, character 9 of Yoshizawa 2011)

A fusion of humeral plate and basisubcostale in the dorsal area is only found in the Psocoptera and Thysanoptera investigated.

118 Anterior margin of ventral basisubcostale: (0) normal; (1) with keel along anterior margin (character 47 of Wipfler *et al.* 2015, character 10 of Yoshizawa 2011)

The usually smooth basisubcostale has a distinct ridge along its anterior margin in Plecoptera, Dermaptera and Hymenoptera investigated (Yoshizawa 2011).

119 Basal hinge: (0) running between posterior notal wing process and 3Ax; (1) running between notum and posterior notal wing process (character 48 of Wipfler *et al.* 2015, character 11 of Yoshizawa 2011)

The basal hinge or folding line usually runs through the articulation of the third axillary and the posterior notal wing process. Instead, the basal hinge may run between notum and posterior notal wing process, when the posterior notal wing process is separated from the notum (Yoshizawa 2011). Among the taxa investigated, the latter condition is found in the Holometabola as well as in Zoraptera and Embioptera.

120 Articulation between anterior notal wing process and 1Ax: (0) almost at a point; (1) along long margin of neck of 1Ax (character 49 of Wipfler *et al.* 2015, character 12 of Yoshizawa 2011)

The articulation between the anterior notal wing process and the first axillary may be restricted to a very short, almost point-like area or extend along the margin of the neck of the first axillary (Yoshizawa 2011).

121 Articulation between antemedian notal wing process and 1Ax: (0) absent; (1) present, side-by-side; (2) present, AmNWP placed over 1Ax (character 50 of Wipfler *et al.* 2015, character 13 of Yoshizawa 2011)

After Wipfler (2014) and Yoshizawa (2011), an articulation between the antemedian notal wing process and the first axillary is present in the majority of Polyneoptera. Only in Caelifera, the antemedian notal wing process is placed of the first axillary (Wipfler *et al.* 2015).

122 Median notal wing process (if missing, lateral notal margin) and body of 1Ax: (0) median notal wing process placed over 1Ax; (1) side-by-side (character 51 of Wipfler *et al.* 2015, character 14 of Yoshizawa 2011)

As with the antemedian notal wing process, also the median notal wing process may be articulated with the first axillary in different ways, sometimes overlapping the body of the 1Ax. This state is found in Ephemeroptera, Blattodea and Psocoptera (Wipfler *et al.* 2015).

123 Proximal tail of body of 1Ax: (0) short; (1) long, articulated with median notal wing process along long margins; (2) long, articulated with median notal wing process at a point (character 52 of Wipfler *et al.* 2015, character 15 of Yoshizawa 2011)

With the exception of Phasmatodea, all Polyneoptera have a long proximal tail of the body of the first axillary that articulates with the median notal wing process along long margins, which was found to represent an apomorphy of Polyneoptera (Yoshizawa 2011). Only in Mantodea, this articulation is present at a point (Yoshizawa 2011).

124 1Ax and posterior notal wing process: (0) separated; (1) fused (character 53 of Wipfler *et al.* 2015, character 16 of Yoshizawa 2011)

The posterior notal wing process and the first axillary are usually widely separated (Snodgrass 1935; Yoshizawa & Saigusa 2001; Hörnschemeyer 2002). Only in Embioptera, the posterior elongation of the first axillary is fused to the posterior notal wing process (Yoshizawa 2011).

125 Head of 1Ax: (0) normal; (1) enlarged (character 54 of Wipfler *et al.* 2015, character 17 of Yoshizawa 2011)

Among the taxa investigated, an enlarged head of the head of the first axillary is found in Zoraptera, Embioptera, and Neuroptera (Yoshizawa 2011).

126 Neck of 1Ax: (0) sclerotized; (1) membranous (character 55 of Wipfler *et al.* 2015, character 18 of Yoshizawa 2011)

In the ground pattern of Pterygota the first axillary most likely forms a single uniform sclerite (Snodgrass 1935). Among the investigated taxa, only in Caelifera the head of the first axillary is separated from the body by a membranous neck area (Yoshizawa 2011).

127 Anteroproximal corner of body of 1Ax: (0) without flap; (1) with flap forming socket-like structure extending over antemedian notal wing process (character 56 of Wipfler *et al.* 2015, character 19 of Yoshizawa 2011)

Only in Plecoptera and Dermaptera the first axillary has an extension of the anterior proximal corner of its body that covers the antemedian notal process (Yoshizawa 2011).

128 Articulation between 1Ax and basisubcostale: (0) present; (1) absent (character 57 of Wipfler *et al.* 2015, character 20 of Yoshizawa 2011)

An articulation between the first axillary and the basisubcostale is usually present among Pterygota (Yoshizawa & Saigusa 2001; Willkommen & Hörnschemeyer 2007; Yoshizawa 2011). Only in Phasmatodea and Caelifera this articulation is absent (Yoshizawa 2011).

129 1Ax and basiradiale: (0) separated; (1) partly fused (character 58 of Wipfler *et al.* 2015, character 21 of Yoshizawa 2011)

Among the investigated taxa, a first axillary and a basiradiale that are partly fused is solely found in Phasmatodea (Yoshizawa 2011).

130 Basiradiale and head of 1Ax: (0) not articulated; (1) articulated (character 59 of Wipfler *et al.* 2015, character 22 of Yoshizawa 2011)

Only in a few investigated taxa (Plecoptera, Dermaptera, Ensifera, Zoraptera, and Embioptera), a fusion of the basiradiale with the 1Ax or an articulation with its head are present (Yoshizawa 2011).

131 1Ax and 2Ax: (0) fused; (1) separated (character 60 of Wipfler *et al.* 2015, character 23 of Yoshizawa 2011)

The first and the second axillary are usually articulated in some way (Snodgrass 1935; Yoshizawa 2011). However, in winged Phasmatodea both sclerites are fused (Yoshizawa 2011).

132 1Ax and anteroproximal corner of 2Ax: (0) closely related; (1) clearly separated by membrane (character 61 of Wipfler *et al.* 2015, character 24 of Yoshizawa 2011)

The clear separation of the first axillary and the anteroproximal corner of the second axillary was found to be an apomorphic character of Dictyoptera (Mantodea + Blattodea) by Yoshizawa (2011).

133 Bending region of basiradiale: (0) broad; (1) constricted; (2) membranous (character 62 of Wipfler *et al.* 2015, character 25 of Yoshizawa 2011)

The basiradiale is usually distinctly bent on its way from the contact area to an axillary sclerite (the first or the second axillary) to the wing (Yoshizawa 2011). Whereas this bending region is broad in the majority of investigated taxa, it is constricted in Orthoptera, and membranous in Zoraptera and Thysanoptera (Yoshizawa 2011).

134 Basiradiale, distal to convex axillary folding line: (0) without membranous region; (1) with membranous region (character 63 of Wipfler *et al.* 2015, character 26 of Yoshizawa 2011)

The convex axillary folding line may cross the basiradiale. In this case, the sclerite may show a membranous area distal to this crossing. This is the case in the Dermaptera, Psocoptera and Holometabola investigated (Yoshizawa & Saigusa 2001; Yoshizawa 2011).

135 Basisubcostale and 2Ax: (0) widely separated; (1) closely approximated (character 64 of Wipfler *et al.* 2015, character 27 of Yoshizawa 2011)

The basisubcostale and the second axillary are widely separated in most Pterygota (Yoshizawa 2011). Only in *Megacrania* (Phasmatodea), in the majority of Caelifera (Orthoptera), as well as in Psocoptera and Thysanoptera, both sclerites are closely approximated (Yoshizawa 2011).

136 2Ax: (0) flat; (1) swollen dorsally (character 65 of Wipfler *et al.* 2015, character 28 of Yoshizawa 2011)

Usually, the second axillary sclerite is of a flat form (Yoshizawa 2011). Only in Psocoptera and Thysanoptera, its dorsal part is distinctly swollen (Yoshizawa 2011).

137 Position of basalare: (0) extended over dorsal region; (1) restricted to ventral region (character 66 of Wipfler *et al.* 2015, character 37 of Yoshizawa 2011)

The basalare, is usually placed placed in the ventral region of the neopteran wing base (Yoshizawa 2011). Instead, it is situated in a more dorsal region extending onto the anterior margin of the wing base in Odonata and Ephemeroptera (Yoshizawa 2011).

138 Articulation between basalare and humeral plate: (0) along broad margins; (1) at a point; (2) loosely related; (3) completely absent (character 67 of Wipfler *et al.* 2015, character 38 of Yoshizawa 2011)

The basalare and the humeral plate are usually articulated (Yoshizawa & Saigusa 2001; Yoshizawa 2011). Only in Holometabola and Thysanoptera both sclerites are clearly separated and no articulation is present (Yoshizawa 2011).

139 Articulation between basalare and ventral basisubcostale: (0) absent; (1) present (character 68 of Wipfler *et al.* 2015, character 39 of Yoshizawa 2011)

An articulation between the basalare and the ventral part of the basisubcostale is only present Psocoptera, Thysanoptera, and Neuroptera (Yoshizawa 2011).

140 Posterior corner of basalare: (0) not strongly swelling; (1) strongly swelling (character 69 of Wipfler *et al.* 2015, character 40 of Yoshizawa 2011)

The basalar sclerite is of variable shape. A conspicuous swelling of the posterior area can be found in Dictyoptera, Embioptera, and Dermaptera, as well as in Psocoptera and Neuroptera (Yoshizawa 2011).

141 Pleural wing process (PWP): (0) articulated with ventral 2Ax; (1) articulated with ventral BSc; (2) articulated with1Ax (character 70 of Wipfler *et al.* 2015, character 41 of Yoshizawa 2011)

The pleural wing process articulates with the second axillary in the majority of Pterygota (Yoshizawa 2011). Only in a very few taxa, this situation has been modified. In Zoraptera, the pleural wing process articulates with the ventral part of the basisubcostale (Yoshizawa 2011). In Neuroptera, the pleural wing process articulateswith the first axillary (Yoshizawa 2011).

Results of the phylogenetic analysis

The cladistic analysis of 141 morphological characters of the thorax, including characters of the wing and wing base, yielded a single most parsimonious cladogram with 389 steps (CI 0,422; RI 0,737). Several taxa were recovered monophyletic with good bremer support: Holometabola, Paranoptera, Polyneoptera, Phasmatodea, Dictyoptera, Xenonomia and Orthoptera (Fig. 25). The data matrix is found in Supplementary Table 2. In the following, apomorphies for all nodes in the cladogram (white circles in Fig. 25) are listed. Hereafter, generic names of the investigated taxa are solely listed, when a character is different in representatives of a monophyletic taxon (e.g. only in the phasmid *Megacrania*, not *Timema*). Otherwise, only taxon names, like e.g. Phasmatodea, corresponding to that

in Fig. 25 and 26 are used. Unambiguous apomorphies are marked in bold. Characters of the wing and wing base (characters 103 to 141) are marked in blue colour in the text.

Node 1: Holometabola [Bremer Support (BS) 7]

25.1: mesosternum invaginated

35.1: mesocoxae closely adjacent medially

39.1: metasternum invaginated

47.1: metacoxae closely adjacent medially

83.1: IIpcm6 present

94.1: IIIppm1 present (also present in Plecoptera, *Megacrania*, tettigonioid clade, reversal in *Troglophilus*)

97.0: IIIpcm5 absent (also absent in *Megacrania* and Caelifera)

119.1: basal hinge running between notum and posterior notal wing process (convergent presence in Mystroptera (= Embioptera + Zoraptera))

134.1: basiradiale distal to convex axillary folding line with membranous region (convergent presence in Psocoptera and Dermaptera)

Node 2: Neuroptera + Hymenoptera [BS 1]

12.2: profurcal arm and pleural apophysis firmly fused (also fused in Psocoptera, Blattodea, Caelifera and grylloid clade)

25.1: ventral mesosternal process forming sternocoxal joint present

36.1: pleural arm of metathorax present (also present in Thysanoptera, Zoraptera, Dermaptera, *Megacrania*, Dictyoptera, Orthoptera, Xenonomia)

40.1: ventral metasternal process forming sternocoxal joint present

Node 3: Paraneoptera + Polyneoptera [BS 1]

12.1: profurcal arm and pleura not fused, connected by muscle (character change [state 0] in Embioptera and at node 27 (reversal in Anostostomatidae); character change [state 2] in Blattodea, Caelifera (different in Tridactylidae), grylloid clade)

16.1: prospina present (also present in Hymenoptera, absent in *Megacrania*)

112.1: posterior notal wing process fused to notum (reversal in Zoraptera and Orthoptera)

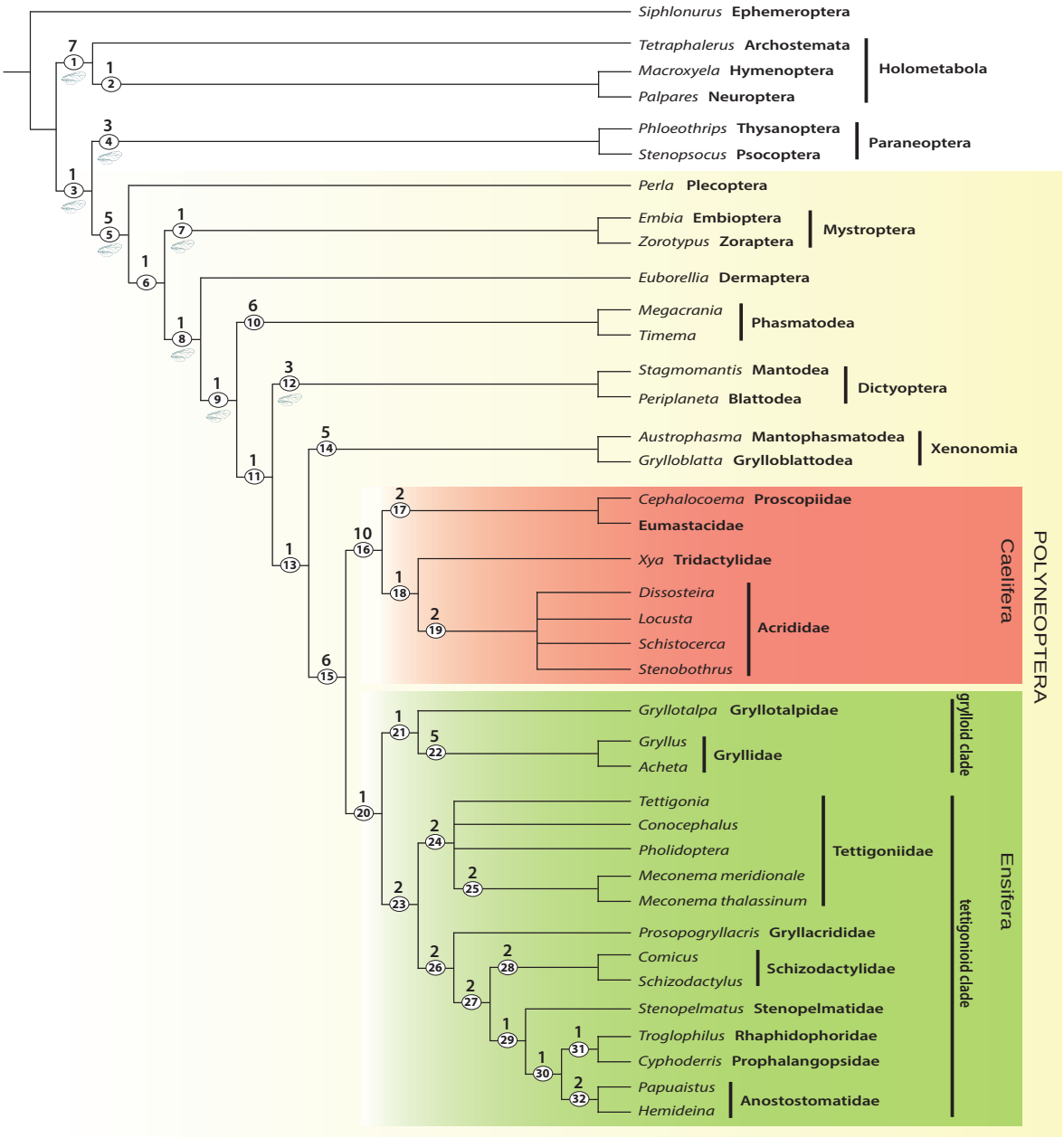


Figure 25. Single most parsimonious tree (tree length 389; CI 0,422; RI 0,737) based on 141 morphological characters. Arabic numbers above branches are Bremer support indices. Potential apomorphies for each clade (numbers in white circles) are presented in the text. Clades supported by characters of the wing and wing base are marked by a wing symbol.

Node 4: Paraneoptera (Thysanoptera + Psocoptera) [BS 3]

71.0: Iscm2 absent (also absent in Dermaptera, Blattodea, Grylloblattodea, and Caelifera)

81.1: IIpcm1 present (also present in Dermaptera, Blattodea, *Megacrania*, Ensifera)

117.1: humeral plate and dorsal basisubcostale fused

135.1: basisubcostale and 2ax closely approximated (also in *Megacrania*, Caelifera ?, inapplicable to Proscopiidae + Eumastacidae)

136.1: 2ax swollen dorsally

139.1: articulation between basalare and ventral basisubcostale present (also present in Neuroptera)

Node 5: Polyneoptera [BS 5]

3.1: dorsal cervical sclerites present (reversal in Dermaptera, *Megacrania*, Xenonomia, Tridactylidae, tettigonioid clade, secondary presence in *Troglophilus*)

8.1: prothoracic anapleural ridge present (reversal Zoraptera, *Megacrania*, Blattodea)

73.1: IIdvm2 present (reversal in *Timema* and *Comicus*)

87.1: IIscm3 present (reversal in Dermaptera and Dictyoptera)

100.1: IIIscm3 present (? in Blattodea and *Schizodactylus*)

115.1: humeral plate (dorsal) membranous

121.1: articulation between antemedian notal wing process and 1ax present side-by-side (absent in Zoraptera; character change [state 2] in Caelifera ?, inapplicable for Proscopiidae and Eumastacidae)

122.1: proximal tail of body of 1ax long, articulated with median notal wing process along long margins (character change [state 0] in *Megacrania*; character change [state 2] in Mantodea)

130.1: basiradiale and head of 1ax articulated (reversal in Dictyoptera and *Megacrania*; ? in Caelifera)

138.1: articulation between basalare and humeral plate at point (character change [state 0] in Mantodea; character change [state 2] in Caelifera ?; inapplicable for Proscopiidae and Eumastacidae)

Node 6: Pliconeoptera or Paurometabola [BS 1]

1.1: two pairs of lateral cervical sclerites present (also present in Neuroptera and Psocoptera; character change [state 0] in Ensifera, reversal in Schizodactylidae)

20.0: median mesonotal suture absent (? in Dictyoptera, Dermaptera, Embioptera, Thysanoptera, Neuroptera, and Archostemata)

29.0: mesospina on distinct spinasternite (reversal in Mantophasmatodea and Orthoptera, ? in Zoraptera)

67.1: Ivlm6 present (reversal in *Megacrania*, Mantodea and Caelifera; also present in Psocoptera)

93.1: IIIdvm3 present (reversal at node 13 (Xenonomia + Orthoptera), ? in Mantophasmatodea; also present in Neuroptera)

Node 7: Mystroptera (Zoraptera + Embioptera) [BS 1]

113.1: tegula strongly sclerotized (? in Ephemeroptera)

119.1: basal hinge between notum and posterior notal wing process (also present in Holometabola)

125.1: head of 1ax enlarged (? in Ephemeroptera, Thysanoptera, and Caelifera)

Node 8: Dermaptera, Phasmatodea, Dictyoptera, Xenonomia, and Orthoptera [BS 1]

92.0: IIIdvm1 absent (reversal in Acrididae, ? in *Schizodactylus*)

106.1: folding of vannus pleated

Node 9: Phasmatodea, Dictyoptera, Xenonomia, and Orthoptera [BS 1]

23.1: invagination of mesopleural arm ventrad in direct proximity to pleural condylus (character change [state 2] in Xenonomia)

38.1: invagination of metapleural arm ventrad in direct proximity to pleural condylus (character change [state 2] in Xenonomia)

62.1: Ispm2 present (also present in Psocoptera and Zoraptera; reversal in Orthoptera; secondary presence in Tettigoniidae)

104.1: costal cross veins more than five (also present in Ephemeroptera, Neuroptera, and Plecoptera; reversal in Blattodea)

Node 10: Phasmatodea [BS 6]

6.1: prothoracic defense glands present

41.1: metasternum and first abdominal sternum fused

63.1: origin of Ispm2 laterally on posterior sternal plate

75.1: IIdvm9 present (? in Hymenoptera and *Schizodactylus*)

78.1: pterothoracic tpm13 present

88.0: IIscm4 absent (also absent in Neuroptera and Blattodea)

90.0: IIscm6 absent (also absent in Ephemeroptera and Grylloblattodea)

101.0: IIIscm4 absent (also absent in Neuroptera, Psocoptera, and Plecoptera)

Node 11: Dictyoptera, Xenonomia, and Orthoptera [BS 1]

22.1: pleural arm of mesothorax arm-like structure projecting in thoracic cavity (as small process in Grylloblattodea)

37.1: pleural arm of metathorax arm-like structure projecting in thoracic cavity (as small process in Grylloblattodea)

89.1: IIscm5 present (also present in Embioptera; absent in Tridactylidae)

Node 12: Dictyoptera [BS 3]

87.0: IIscm3 absent (also absent in Dermaptera)

120.1: articulation of anterior notal wing process and 1ax along long margin of neck of 1ax (also present in Ephemeroptera and Hymenoptera)

132.1: 1ax and anteroproximal corner of 2ax clearly separated by membrane (? in Thysanoptera)

140.1: posterior corner of basalare strongly swelling (also present in Neuroptera, Psocoptera, Dermaptera, and Embioptera)

Node 13: Xenonomia and Orthoptera [BS 1]

5.1: pronotum and propleura laterally partly or completely connected (also present in Psocoptera, Embioptera, and *Timema*)

86.0: IIscm2 absent (? in *Schizodactylus*, *Acheta*, and Hymenoptera)

93.0: IIIdvm3 absent (secondary absence; ? in Mantophasmatodea and *Schizodactylus*)

Node 14: Xenonomia [BS 5]

3.0: dorsal cervical sclerites absent (secondary absence, also secondarily absent in Dermaptera, Megacrania, Tridactylidae, tettigonioid clade (secondary presence in *Troglophilus*)

9.1: prothoracic anapleural invagination or wing present

15.0: posterior branch of profurca as short process

23.2: invagination of mesopleural arm posterad to pleural ridge, internal processus of epimeron

38.2: invagination of metapleural arm posterad to pleural ridge, internal processus of epimeron

99.0: IIIscm2 absent (? in *Schizodactylus*)

102.1: IIIscm5 present (? in Ephemeropera and *Schizodactylus*)

103.0: wings absent (also absent in *Timema*, and several times within Orthoptera)

Node 15: Orthoptera [BS 6]

4.1: pronotum saddle-like, cryptopleura

10.2: connection of propleura and prosternum as pleurosternal bridge (also present in Mantodea)

24.1: pterothoracic furcae enclosing respective pleural arm from ventral side

30.1: mesospina and mesofurcae situated in one line on sternacosta

31.1: mesospina stalked with distal plate and/or processi

44.1: lateral process of metafurca strongly curved and spatulate (modification within Orthoptera: Acrididae, Proscopiidae + Eumastacidae plate-like; Tettigoniidae wing-like; node 27 arm-like or flat extension)

59.0: Itpm3 absent (also absent in Thysanoptera)

60.0: Itpm4 absent (also absent in Ephemeroptera and Archostemata; reversal in Gryllidae)

62.0: secondary absence of Ispm2 (reversal in Tettigoniidae)

Node 16: Caelifera [BS 10]

19.1: prospina on posterior part of basisternum or connected with furca (also present in Embioptera and Meconematinae)

27.1: anterior processus of mesofurca present (also present in Mantophasmatodea, Psocoptera, and Neuroptera)

43.1: anterior process of metafurca triangular forming transition to lateral furcal arm (not applicable to Tridactylidae)

48.0: Idlm5 absent (also absent in Dermaptera, ? in *Timema* and *Schizodactylus*)

49.1: Idvm6 duplicated

67.0: secondary absence of Ivlm6 (secondarily absent also in *Megacrania* and Mantodea)

71.0: Iscm2 absent (also absent in Paraneoptera, Dermaptera, Blattodea, and Grylloblattodea)

80.0: secondary absence of IIspm3 (secondarily absent also in *Comicus* and *Troglophilus*)

82.0: IIpcm5 absent (also absent in Thysanoptera and Neuroptera)

91.0: secondary absence of IIscm7 (secondarily absent also in *Megacrania* and Mantodea)

97.0: IIIpcm5 absent (also absent in *Megacrania* and Holometabola)

Node 17: Proscopiidae and Eumastacidae [BS 2]

84.0: secondary absence of IIvlm3 (secondarily absent also in *Megacrania*)

103.0: wings absent (also absent in Xenonomia, *Timema*, and within Ensifera)

Node 18: Tridactylidae and Acrididae [BS 1]

74.0: IIdvm8 absent (also absent in Ephemeroptera, Neuroptera, Mantophasmatodea, Tettigoniidae, and Rhaphidophoridae + Prophalangopsidae)

Node 19: Acrididae [BS 2]

44.3: lateral process of metafurca as broad, tapering dorsolaterally projecting plate

70.1: Ivlm10 present (also present in Eumastacidae)

85.1: IIvlm3 as sclerotized fiber

92.1: secondary presence of IIIdvm1

Node 20: Ensifera [BS 1]

1.0: secondary presence of single pair of lateral cervical sclerites (reversal in Schizodactylidae)

79.1: IIppm1 present (also present in Neuroptera, Plecoptera, and *Megacrania*)

Node 21: grylloid clade [BS 1]

58.1: ltpm2_2 present

69.1: Ivlm8 unpaired

Node 22: Gryllidae [BS 5]

11.2: prothoracic furcasternite freestanding paired sclerite

42.0: secondary presence of metafurca with single lateral arm-like extension (secondarily present also in Tridactylidae)

56.1: ldvm19 with two bundles, the anterior running behind cryptopleura

60.1: secondary presence of ltpm4

65.1: Ipcm2 present (also present in Hymenoptera, Psocoptera, Grylloblattodea, Tridactylidae, Tettigoniidae, and node 30)

Node 23: tettigonioid clade [BS 2]

3.0: secondary absence of dorsal cervical sclerites (secondarily absent also in Dermaptera, *Megacrania*, Xenonomia, and Tridactylidae; reversal in Rhaphidophoridae)

94.1: IIIppm1 present (also present in Holometabola, Plecoptera, and *Megacrania*; reversal in Rhaphidophoridae)

Node 24: Tettigoniidae [BS 2]

44.2: lateral process of metafurca wing-like, bent

62.1: secondary presence of Ispm2 (61): absent --> present

63.2: origin of Ispm2 laterally on spinasternite

65.1: Ipcm2 present (also present in Hymenoptera, Psocoptera, Grylloblattodea, Tridactylidae, Gryllidae, and node 30)

74.0: IIdvm8 absent (also absent in Ephemeroptera, Neuroptera, Mantophasmatodea, Tridactylidae + Acrididae, and Rhaphidophoridae + Prophalangopsidae)

Node 25: Meconematinae [BS 2]

19.0: prospina on posterior part of basisternum or connected with furca (also present in Embioptera and Caelifera)

50.1: Idvm9 present (also present in Archostemata, Hymenoptera, and node 27)

Node 26: Gryllacrididae, Schizodactylidae, Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, Anostostomatidae [BS 2]

15.2: posterior branch of profurca as arm-like tapered process (also present in Gryllotalpidae)

18.1: stalked prospina with paired posterior processus (reversal in Prophalangopsidae)

95.1: IIIspm5 present (also present in Mantophasmatodea; reversal in Stenopelmatidae)

Node 27: Schizodactylidae, Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, Anostostomatidae [BS 2]

12.0: profurcal arm and propleura not connected (as secondary state; reversal in Anostostomatidae)

44.0: lateral process of metafurca as arm-like, tapered conical or flat extension (as secondary state)

50.1: Idvm9 present (also present in Archostemata, Hymenoptera, and Meconematinae)

Node 28: Schizodactylidae [BS 2]

1.1: secondary presence of two pairs of lateral cervical sclerites

19.2: prospina on anterior part of mesosternum

33.1: lateral processi of stalked mesospina: with single laterally processus per body side, t-shaped

Node 29: Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae [BS 1]

45.1: dorsal process of metafurca present

Node 30: Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae [BS 1]

65.1: Ipcm2 present (also present in Hymenoptera, Psocoptera, Grylloblattodea, Tridactylidae, Gryllidae, and Tettigoniidae)

Node 31: Rhaphidophoridae and Prophalangopsidae [BS 1]

74.0: IIdvm8 absent (also absent in Ephemeroptera, Neuroptera, Mantophasmatodea, Tridactylidae + Acrididae, and Tettigoniidae)

Node 32: Anostostomatidae [BS 2]

12.1: profurcal arm and propleura not fused, connected by muscle (as secondary state)

61.1: Itpm7 present

The cladistic analysis of 102 morphological characters of the thorax, excluding characters of the wing and wing base, yielded 13 equally parsimonious cladograms with 291 steps each (CI 0,402; RI 0,748). Holometabola, Phasmatodea, Xenonomia and Orthoptera are found to be monophyletic groups in the strict consensus tree with good bremer support (Fig. 26). The data matrix is found in Supplemenary Table 2. In the following, common apomorphies of the parsimonious trees for all nodes (white circles in Fig. 26) in the strict consensus tree are listed. Unambiguous apomorphies are marked in bold. Characters that reflect apomorphies for the respective clade in only some of the parsimonious trees are listed separately. These characters represent e.g. an apomorphy of a broader defined taxon in at least one of the equally parsimonious cladograms.

Node 1: Holometabola [BS 5]

25.1: mesosternum invaginated

35.1: mesocoxae closely adjacent medially

39.1: metasternum invaginated

47.1: metacoxae closely adjacent medially

82.1: IIpcm6 present (? in Hymenoptera)

97.0: IIIpcm5 absent (also absent in *Megacrania* and Caelifera)

some trees:

2.1: cervical sclerites and pleura partly or completely fused (? in Archostemata)

88.0: IIscm4 absent (also absent in Blattodea and Neuroptera)

Node 2: Phasmatodea [BS 4]

6.1: prothoracic defense glands present

40.1: metasternum and abdominal sternum 1 fused

63.2: origin of Ispm2 laterally on spinasternite

75.1: IIdvm9 present

78.1: pterothoracic tpm13 present

90.0: IIscm6 absent (also absent in Grylloblattodea and Ephemeroptera)

101.0: IIIscm4 absent (also absent in Psocoptera, Neuroptera, and Plecoptera)

some trees:

88.0: IIscm4 absent (also absent in Blattodea and Neuroptera)

Node 3: Xenonomia and Orthoptera [BS 1]

86.0: IIscm2 absent

some trees:

5.1: pronotum and propleura laterally partly or completely connected (also present in Psocoptera, Embioptera, and *Timema*)

93.0: IIIdvm3 absent (also absent in Plecoptera, Psocoptera, Thysanoptera, Hymenoptera, and Archostemata); ? in Mantophasmatodea and *Schizodactylus*)

Node 4: Xenonomia [BS 5]

9.1: prothoracic anapleural invagination or wing (paracoxal process in Wipfler *et al.* 2015) present

15.0: posterior branch of profurca as short process

23.2: invagination of mesopleural arm posterad to pleural ridge, internal processus of epimeron

38.2: invagination of metapleural arm posterad to pleural ridge, internal processus of epimeron

99.0: IIIscm2 absent

102.1: IIIscm5 present

some trees:

10.3: connection of propleura and prosternum mainly membranous (also membranous in Ephemeroptera and Thysanoptera)

Node 5: Orthoptera [BS 5]

4.1: pronotum saddle-like, cryptopleura

10.2: connection of propleura and prosternum as pleurosternal bridge (also in Mantodea)

24.1: mesofurca enclosing mesopleural arm from ventral side

30.1: mesospina and mesofurcae situated in one line on sternacosta

31.1: mesospina stalked with distal plate and/or processi

44.1: lateral process of metafurca strongly curved and spatulate (modification within Orthoptera: Acrididae, Eumastacidae + Proscopiidae plate-like; Tettigoniidae wing-like; node 16 arm-like or flat extension)

59.0: Itpm3 absent (also absent in Thysanoptera)

60.0: Itpm4 absent (also absent in Ephemeroptera and Archostemata; reversal in Gryllidae)

some trees:

62.0: Ispm2 absent (also absent in Ephemeroptera, Plecoptera, Dermaptera, Embioptera, Thysanoptera, and Holometabola; reversal in Tettigoniidae)

68.1: Ivlm8 present (also present in Psocoptera, Mantodea, and Blattodea; reduced in *Papuaistus* and *Comicus*)

Node 6: Caelifera [BS 8]

19.1: prospina on posterior part of the basisternum or connected with furca (also present in Embioptera and Meconematinae)

48.0: Idlm5 absent (also absent in Dermaptera)

49.1: Idvm6 duplicated

67.0: secondary absence of Ivlm6 (secondarily absent also in *Megacrania*)

80.0: secondary absence of IIspm3 (secondarily absent also in *Comicus* and Rhaphidophoridae)

82.0: IIpcm5 absent (also absent in Thysanoptera and Neuroptera)

91.0: secondary absence of IIscm7 (secondarily absent also in *Megacrania*)

97.0: IIIpcm5 absent (also absent in *Megacrania* and Holometabola)

some trees:

14.0: secondary presence of profurca with single furcal arm (also in Rhaphidophoridae)

27.1: anterior process of mesofurca present (also present in Mantophasmatodea, Psocoptera and Neuroptera)

43.1: anterior process of metafurca triangular forming transition to lateral furcal arm (not applicable to Tridactylidae)

71.0: Iscm2 absent (also absent in Paraneoptera, Dermaptera, Blattodea, and Grylloblattodea)

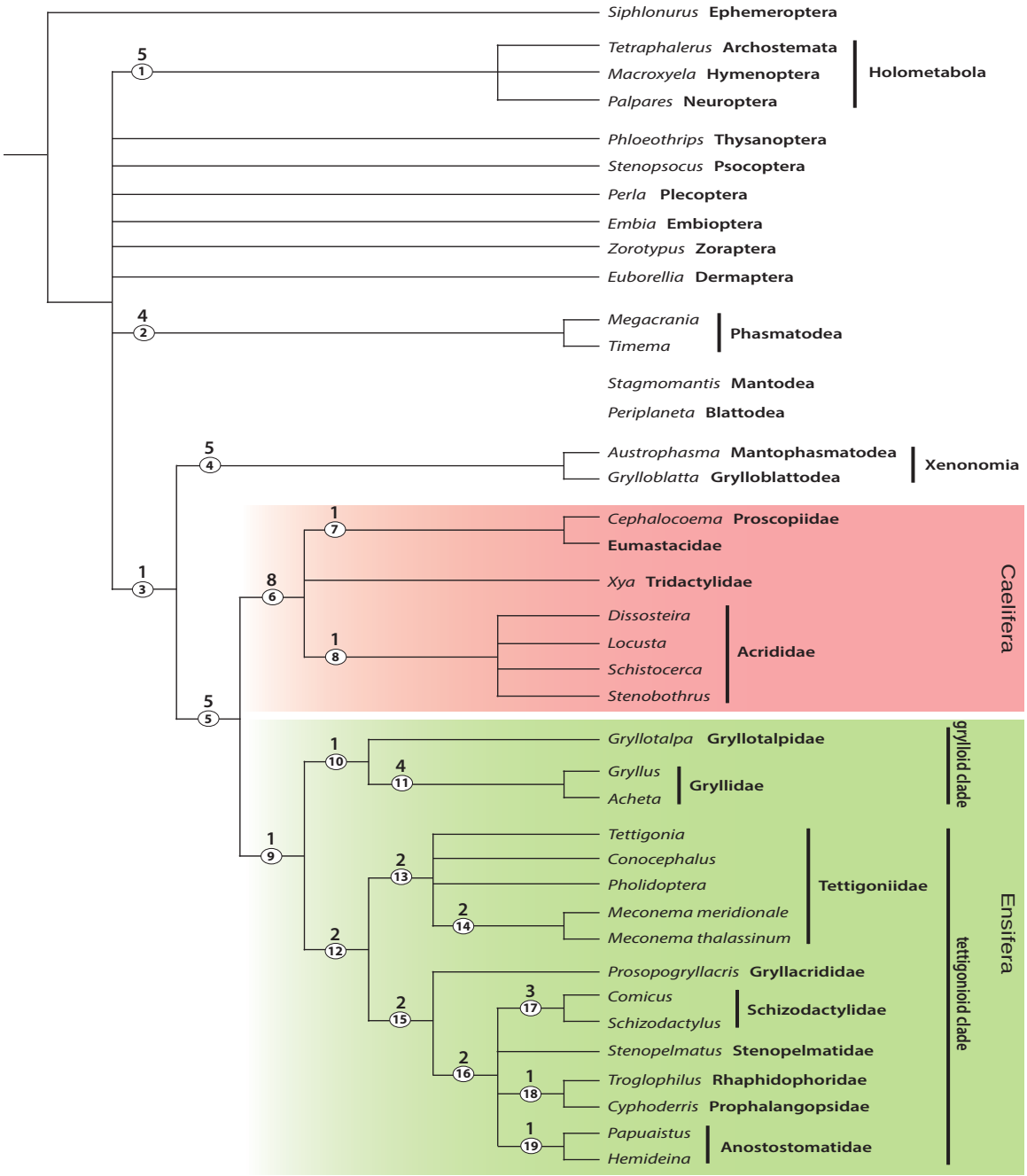


Figure 26. Strict consensus of 13 most parsimonious trees (tree length 291; CI 0,402; RI 0,748) based on 102 morphological characters. Arabic numbers above branches are Bremer support indices. Potential apomorphies for each clade (numbers in white circles) are presented in the text.

Node 7: *Cephalocoema* (Proscopiidae) and Eumastacidae [BS 1]

84.0: IIvlm3 absent (also absent in *Megacrania* and Ephemeroptera)

some trees:

57.0: secondary absence of Itpm2 (secondarily absent also in Rhaphidophoridae)

Node 8: Acrididae [BS 1]

92.1: IIIdvm1 present (secondary presence)

some trees:

44.3: lateral process of metafurca as broad tapering dorsolaterally projecting plate (? for Proscopiidae and Eumastacidae)

70.1: Ivlm10 present (also present in Eumastacidae)

85.1: IIvlm3 as sclerotized fiber (not applicable to other Caelifera)

Node 9: Ensifera [BS 1]

1.0: lateral cervical sclerite as single pair (secondary presence; two pairs in Schizodactylidae)

79.1: IIppm1 present (also present in Plecoptera, *Megacrania* and Neuroptera)

Node 10: grylloid clade [BS 1]

58.1: Itpm2_2 present

69.1: Ivlm8 unpaired

Node 11: Gryllidae [BS 4]

11.2: prothoracic furcasternite as freestanding paired sclerite

42.0: metafurca with single arm-like extension (secondary presence; also secondarily present in Tridactylidae)

56.1: Idvm19 with two bundles, the anterior running behind cryptopleura

60.1: secondary presence of Itpm4

some trees:

65.1: Ipcm2 present (also present in Hymenoptera, Psocoptera, Grylloblattodea, Tridactylidae, Tettigoniidae, Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae)

Node 12: tettigonioid clade [BS 2]

94.1: IIIppm1 present (also present in Holometabola, Plecoptera and *Megacrania*; reduced in Rhaphidophoridae)

some trees:

3.0: dorsal cervical sclerites absent (reversal in Rhaphidophoridae)

12.1: profurcal arm and pleura connected by muscle (muscle reduced in *Comicus*, Stenopelmatidae, and Rhaphidophoridae)

Node 13: Tettigoniidae [BS 2]

44.2: lateral process of metafurca wing-like, bent, opening oriented anteriorly

62.1: Ispm2 present (also present in Psocoptera, Zoraptera, Mantodea, Blattodea, Phasmatodea and Xenonomia)

63.2: origin of Ispm2 laterally on spinasternite

some trees:

65.1: Ipcm2 present (also present in Hymenoptera, Psocoptera, Grylloblattodea, Tridactylidae, Gryllidae, Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae)

Node 14: Meconematinae [BS 2]

19.0: prospina on posterior part of basisternum or connected with furca (also present in Embioptera and Caelifera)

50.1: Idvm9 present (also present in Archostemata, Hymenoptera, and node 16)

Node 15: Gryllacrididae (Stenopelmatidae, (Rhaphidophoridae + Prophalangopsidae), Anostostomatidae, Schizodactylidae) [BS 2]

15.2: posterior branch of profurca as arm-like tapered process (also present in Gryllotalpidae)

18.1: stalked prospina with paired posterior process (reversal in Prophalangopsidae)

95.1: IIIspm5 present (also present in Mantophasmatodea; reduced in Stenopelmatidae)

Node 16: (Stenopelmatidae, (Rhaphidophoridae + Prophalangopsidae), Anostostomatidae, Schizodactylidae) [BS 2]

44.0: lateral process of metafurca as arm-like tapered or flat extension (secondary presence)

50.1: Idvm9 present (also present in Archostemata, Hymenoptera, and Meconematinae; reduced in Rhaphidophoridae)

some trees:

45.1: dorsal process of metafurca present (also present in Gryllotalpidae; reduced in Schizodactylidae)

Node 17: Schizodactylidae [BS 3]

1.1: two pairs of lateral cervical sclerites (secondary presence)

19.2: prospina on anterior part of mesosternum

33.1: t-shaped mesospina with single lateral processus per body side

45.0: dorsal processus of metafurca absent (secondary absence)

Node 18: Rhaphidophoridae and Prophalangopsidae [BS 1]

74.0: IIIdvm8 absent (also absent in Ephemeroptera, Neuroptera, Mantophasmatodea, Acrididae and Tettigoniidae)

Node 19: Anostostomatidae [BS 1]

61.1: Itpm7 present

some trees:

12.1: profurcal arm and propleura not fused, connected by muscle (secondary presence)

In both analyses, complete and reduced dataset, the monophyly of Orthoptera was recovered and supported by a number of characters. The revealed internal relationships of Orthoptera are almost identical in the two analyses conducted. Table 2 compiles the differences between those two analyses with regard to the morphological characters supporting each node within the Orthoptera. Mostly, all apomorphies supporting a respective orthopteran node in the analysis of the complete dataset (Fig. 25) are also found in the analysis of the reduced dataset (Fig. 26), although some of these apomorphies are only applicable to some of the equally parsimonious trees (see Table 2). Only few characters really differ between the two analyses: e.g. the absence of the dorsal processus of the metafurca in Schizodactylidae is reconstructed as being reduced in that taxon in analysis of the reduced dataset, since this node is not resolved in the tree. In the analysis of the complete dataset on the other hand, the presence of this dorsal processus of the metafurca is reconstructed to be an unambiguous apomorphy to a taxon compiling Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae.

Indeed, the good resolution of the tree received by the analysis of the complete dataset deepens the understanding of evolutionary events related to some characters. For instance in the analysis of the reduced dataset, the muscle Ispm2 (M. prospina-mesopleuralis) is reconstructed to be absent in the last common ancestor of Orthoptera, its presence in Tettigoniidae is secondary. The analysis of the complete dataset provides additional information by reconstructing the absence of Ispm2 in Orthoptera as being secondary.

Table 2. List of characters that differ between the analysis of the complete and the reduced dataset with regard to the sister taxon of Orthoptera and the internal clades of Orthoptera. Characters that are listed under "some trees" in the analysis of the reduced data set mostly coincide with those found by the analysis of the complete data set. Characters that are not listed as apomorphies in the other analysis are underlined.

clade	analysis of the complete data set (tree: Fig. 25)	analysis of the reduced dataset (tree: Fig. 26)
Xenonomia and Orthoptera		*some trees:* 5.1, 93.0
Orthoptera	62.0: secondary absence of Ispm2 (reversal in Tettigoniidae)	*some trees:* 62.0: Ispm2 absent, 68.1
Caelifera		*some trees:* 14.0: secondary presence of profurca with single furcal arm (also in Rhaphidophoridae), 27.1, 43.1, 71.0
Proscopiidae and Eumastacidae	103.0: wings absent	*some trees:* 57.0: secondary absence of Itpm2
Tridactylidae and Acrididae	74.0	-
Acrididae		*some trees:* 44.3, 70.1, 85.1
Ensifera	no differences	
grylloid clade	no differences	
Gryllidae		*some trees:* 65.1
tettigonioid clade	3.0: secondary absence of dorsal cervical sclerites (reversal in Rhaphidophoridae)	*some trees:* 3.0, 12.1: profurcal arm and pleura connected by muscle (character change: 2 to 1)
Tettigoniidae	74.0	*some trees:* 65.1
Meconematinae	no differences	
Gryllacrididae, Schizodactylidae, Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, Anostostomatidae	no differences	
Schizodactylidae, Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, Anostostomatidae	12.0: profurcal arm and propleura not connected (as secondary state; reversal in Anostostomatidae)	*some trees:* 45.1: dorsal process of metafurca present (also present in Gryllotalpidae; reduced in Schizodactylidae)
Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, Anostostomatidae	45.1 (as unambiguous apomorphy)	-
Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae	65.1	-
Rhaphidophoridae and Prophalangopsidae	no differences	
Anostostomatidae		*some trees:* 12.1
Schizodactylidae		45.0: dorsal processus of metafurca absent (secondary absence)

Discussion

The present study expands the knowledge on the thoracic morphology of Neoptera by providing data on further representatives, additional characters and new hypotheses on their internal relationships.

Including yet unstudied ensiferan taxa such as Gryllacrididae and Stenopelmatidae, the herein presented studies on the morphology of the thoracic skeletomuscular system of Orthoptera represent the most comprehensive comparative investigation of this character complex so far.

The ground plan morphology of orthopterans' thoracic skeleton (Fig. 27)

The saddle-shaped pronotum and the internal cryptopleura have always been considered a defining character of Orthoptera and strongly support the assumption of its monophyly (Wipfler *et al.* 2015). The present study presents numerous further characteristics of the thoracic skeleton of Orthoptera that represent apomorphies of this insect lineage: connection of propleura and prosternum as pleurosternal bridge (convergent in praying mantises), pterothoracic furcae that enclose the respective pleural arm from the ventral side, mesofurca and mesospina that are situated in one line at the sternacosta, and a stalked mesospina with a delimited dorsal plate. The majority of the characters coded for the phylogenetic analysis contain anatomical features of the sternal region of the thorax, a character system that was previously suggested to contain phylogenetic information for Orthoptera (Ander 1939; Naskrecki 2000). In a number of these characters, the reconstruction shows different character states for the last common ancestor of Caelifera and Ensifera respectively (Table 3).

The presence of detached lateral cervical sclerites is regarded as an apomorphic trait of Pterygota (Matsuda 1970; Wieland 2006). Nevertheless, there are different opinions about the polarization of this character in pterygote insects. Either, a single lateral cervical sclerite represents the plesiomorphic condition, with multiplied lateral cervical sclerites being the result of secondary partitions of this sclerite (Matsuda 1970; Whiting *et al.* 1997; Wieland 2006; Bradler 2009). Alternatively, the presence of two separated lateral cervical sclerites is assumed to be plesiomorphic (Martin 1916; Crampton 1926; Snodgrass 1935), hence, the occurrence of a single lateral sclerite is subsequently a consequence of

the fusion of the two sclerites or the reduction of one of them. Even a convergent origin of the single lateral sclerite is feasible. In the majority of Polyneoptera, two distinctly separated sclerites are present, namely in Embioptera (Rähle 1970), Phasmatodea (Bradler 2009), Dictyoptera (Wieland 2006), Mantophasmatodea (Wipfler *et al.* 2015), Grylloblattodea (Walker 1938), Zoraptera (Friedrich & Beutel 2008), and Dermaptera (Crampton 1926; Matsuda 1970). Only in Plecoptera, the lateral cervical sclerite appears as a single undivided plate, but it is separated in two parts in *Eusthenia* (Zwick 1980), likely representing the derived condition for this taxon (Matsuda 1970). In contrast to the opinion of Matsuda (1970), the presence of two lateral cervical sclerites is confirmed to be the plesiomorphic state for Orthoptera in the present analysis. In consequence, the presence of a single pair of lateral cervical sclerites is then a derived condition in Ensifera and most likely a consequence of the fusion of the two cervical sclerites found in other Polyneoptera. This is supported by the musculature that is associated with the lateral cervical sclerite. All muscles that are found in association with the cervical sclerites in Caelifera (e.g. Idvm2, Idvm3, Idvm5, Idvm6) are likewise present in the Ensifera with the difference that the respective muscles are here inserted on distant parts of the single lateral cervical sclerite. If the single lateral sclerite of Ensifera was the result of the reduction of one sclerite, the respective muscles would most likely have been lost as well. The presence of dorsal cervical sclerites was considered to be a potential synapomorphy of Polyneoptera (Wipfler *et al.* 2015), although their absence in several subgroups would indicate multiple independent losses within the group (e.g. Xenonomia, Dermaptera). This assumption was confirmed here by the analysis including wing and wing base characters (complete dataset). Although the analysis excluding wing and wing base characters (reduced dataset) does not support a clade Polyneoptera, and the polarization of this characters becomes uncertain for Orthoptera. Nonetheless it is likely that dorsal cervical sclerites were present in the last common ancestor of Orthoptera. Within the investigated Caelifera, only *Xya* (Tridactylidae) lacks dorsal cervical sclerites. Besides, their presence is documented for another species of the Tridactyloidea, *Cylindroryctes spegazzinii* (Cylindrachetidae) (Carpentier 1936), and also for Tetrigidae and Pamphagidae (Alicata 1962). Within the Ensifera, dorsal cervical sclerites are present in the grylloid clade, whereas in the present analysis they are reconstructed to be absent in the last common ancestor of the tettigonioid clade. Hence, the occurrence of this cervical scle-

rite in *Troglophilus* (Rhaphidophoridae) would be a secondary condition. In contrast to other representatives of the Orthoptera (Alicata 1962), the dorsal cervical sclerite in *Troglophilus* is unpaired having a clip-like appearance (Leubner *et al.* 2016). The same morphology is described for the dorsal cervical sclerite of the rhaphidophorid *Dolichopoda geniculata* (Alicata 1962). But only a small dorsal sclerite is present in *Ceuthophilus brevipes* (*precervicale* in Gurney 1935), and no dorsal cervical sclerite is described in *Macropathus filifer* (Richards 1955). Therefore, it is not likely that this unpaired clip-like dorsal cervical sclerite is an autapomorphy of all cave crickets (Rhaphidophoridae), but rather represents a character that evolved within the group.

Table 3. List of characters of the sternal skeleton whose character state differs between Ensifera and Caelifera. The majority of characters have an uncertain state in the last common ancestor of Orthoptera, but a distinct state in the two subtaxa respectively.

Character of the sternal skeleton	**Last common ancestor of Orthoptera**	**Last common ancestor of Caelifera**	**Last common ancestor of Ensifera**
connection of profurcal arm and propleura	uncertain	profurcal arm and propleura firmly fused	uncertain Firmly fused in grylloid clade; connected by muscle in tettigonioid clade (muscle absent in *Troglophilus*, *Cyphoderris* and *Stenopelmatus*)
Profurca	uncertain	with single furcal arm	branched
prospina located	on distinct spinasternite between pro- and mesosternum	on posterior part of basisternum	-
shape of prospina	uncertain	flat median extension ? (different in *Xya*)	stalked, with distal plate and processi
anterior process of mesofurca	absent	present	-
distal part of stalked mesospina	uncertain	without processi	with processi

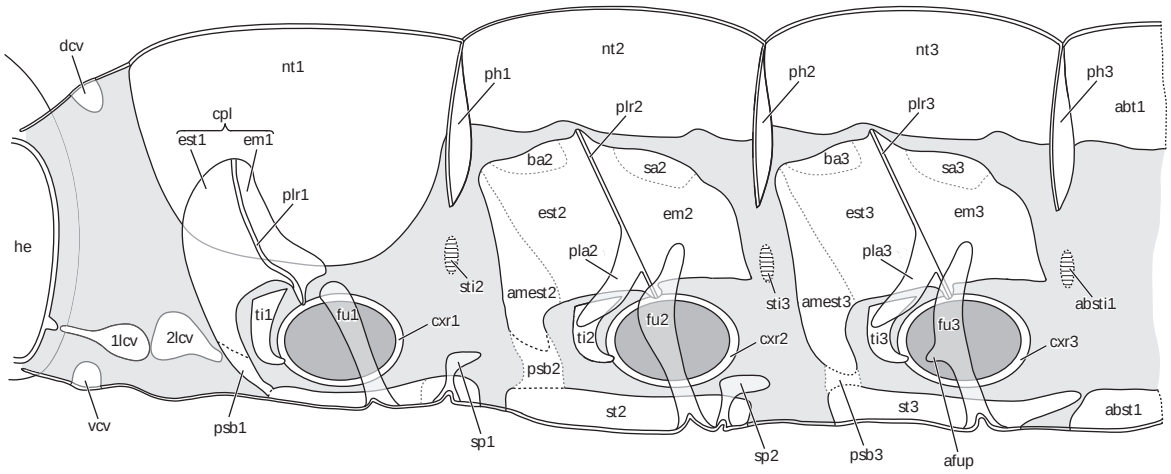


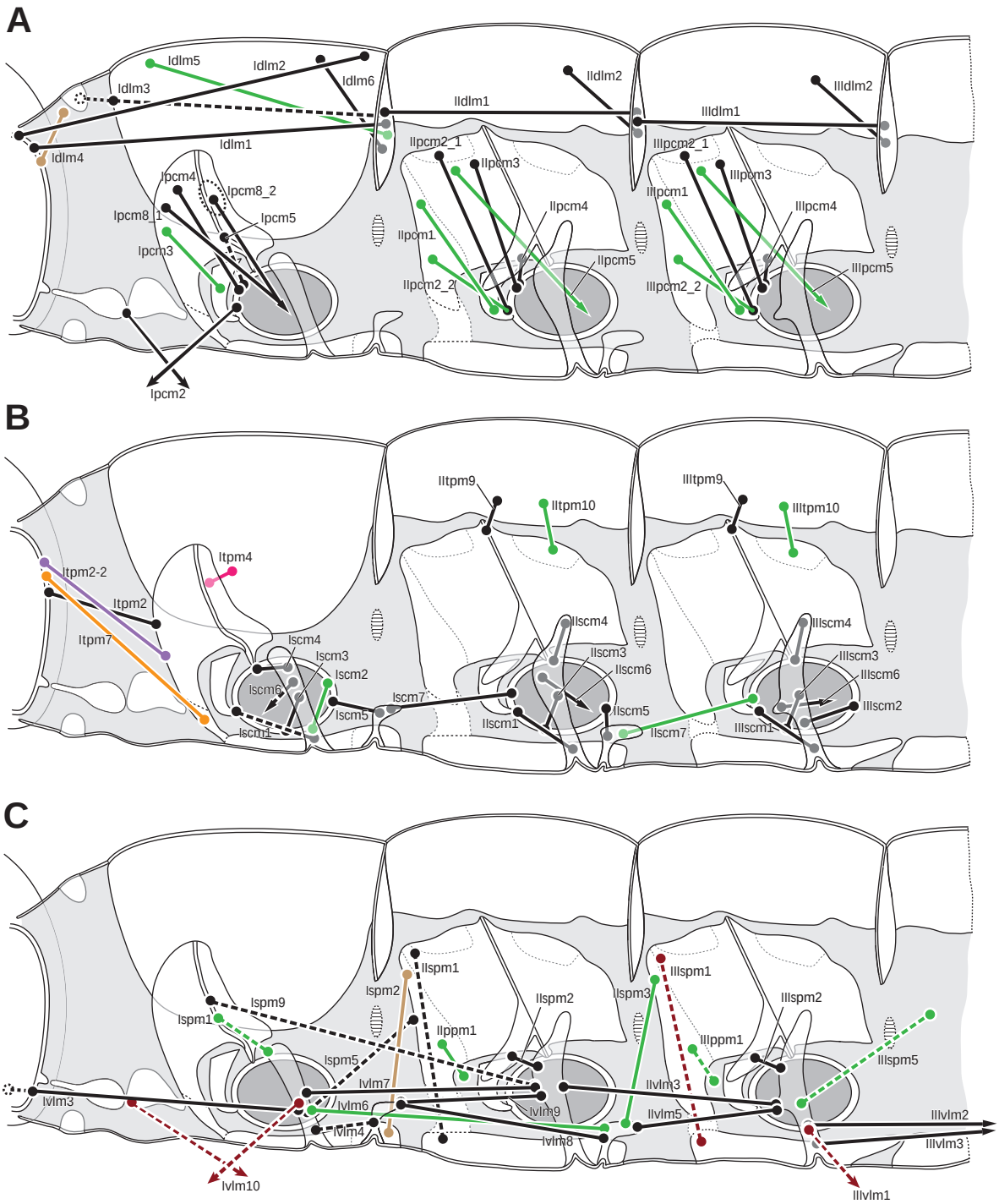
Figure 27. Thoracic skeleton of Orthoptera. Structures in light grey are not present in all members of the Orthoptera. Wing base and associated sclerites (ba, sa) represent the unwinged condition.
1/2lcv first/second lateral cervical sclerite, *abst1* first abdominal sternum, *absti1* first abdominal stigma, *abt1* first abdominal tergum, *afup* anterior furcal process, *amest2/3* anterior margin of mes-/metepisternum, *ba2/3* meso-/metathoracic basalare, *cpl* cryptopleura, *cxr1/2/3* pro-/meso-/metacoxal rim, *dcv* dorsal cervical sclerite, *est1/2/3* pro-/mes-/metepisternum, *em1/2/3* pro-/mes-/metepimeron, *fu1/2/3* pro-/meso-/metafurca, *he* head, *nt1/2/3* pro-/meso-/metanotum, *ph1/2/3* pro-/meso-/metaphragma, *pla2/3* meso-/metapleural arm, *plr1/2/3* pro-/meso-/metathoracic pleurosternal ridge, *psb1/2/3* pro-/meso-/metathoracic pleurosternal bridge, *sa2/3* subalare of meso-/metathorax, *sp1/2* pro-/mesospina, *st1/2/3* pro-/meso-/metasternum, *sti2/3* meso-/metathoracic stigma, *ti1/2/3* pro-/meso-/metatrochantin, *vcv* ventral cervical sclerite.

The ground plan morphology of orthopterans' thoracic musculature (Figs. 28–30)

The total number of thoracic muscles in both subgroups of the Orthoptera is markedly different. In Caelifera it varies between 57 (*Cephalocoema*), 59 (*Xya*) and 65-68 in Acrididae and Eumastacidae. In Ensifera, the vast majority of examined species exhibits around 80 thoracic muscles or even more. Here, the total number varies between 84-92 in Tettigoniidae, 89 or 95 in Gryllidae, 87-88 in Anostostomatidae, 83 in *Gryllotalpa*, 79 in *Stenopelmatus*, and 92 in *Prosopogryllacris*. A decreased number of thoracic muscles is only found in *Comicus* (68) and *Troglophilus* (70). Generally, the number of thoracic muscles is reduced in wingless species in both Caelifera and Ensifera. The exceedingly small number of thoracic muscles in *Comicus* as compared to other ensiferans might be explained by some modifications in the skeletal anatomy characterized by several fused thoracic sclerites (Leubner *et al.* 2017).

The thoracic musculature of Orthoptera provides a meaningful number of useful characters in the present phylogenetic analysis. Some of these muscles are only found in a single subgroup and thereby represent unambiguous autapomorphies of a certain taxon, e.g., the M. prospina-mesopleuralis (Ispm2) for Tettigoniidae (Fig. 28C) or the M. pronoto-apodemalis anterior (Itpm4) in Gryllidae (Fig. 28B). A large number of thoracic muscles are with certainty present in the orthopteran ground pattern (Fig. 28–30). Nevertheless, the complete set of characteristic muscles differs exceedingly between the both major subgroups Caelifera and Ensifera. For example, the muscle IIscm7 (M. mesospina-metacoxalis) is solely present in ensiferans (Fig. 28B), whereas the muscle IIIvlm1 (M. metafurca-spinalis) could only be found in caeliferans (Fig. 28C). In addition, a number of muscles are found in Orthoptera that were not described in the neopteran thorax before (Friedrich & Beutel 2008), e.g. the M. mesofurca-propleuralis (IIspm9, Fig. 28C). This muscle originates on the anterior edge of the mesofurcal arm and inserts at the pleural ridge of the prothoracic cryptopleura. It was only found in two representatives of Orthoptera, in the cave cricket *Troglophilus* (Ensifera) (Leubner *et al.* 2016) and the pygmy mole cricket *Xya* (Caelifera) (Supplementary Plate 45). As this muscle is hitherto only found in these distant orthopteran lineages the most likely explanation is a convergent origin of IIspm9 in both representatives.

The characteristics of some thoracic muscles show interesting correlations between short-horned and long-horned grasshoppers that are elucidated in the following:
The muscle M. procoxa-cervicalis transversalis (Ipcm2) connects the prothoracic coxal rim with the lateral cervical sclerite of the opposite body half (Fig. 28A). Within the Orthoptera this muscle is present in the majority of ensiferan representatives. In contrast, the muscle Ipcm2 is absent in the majority of examined caeliferan species, although it was mistakenly stated to be present in *Dissosteira carolina* by Wipfler *et al.* (2015). This muscle of *Dissosteira* was originally described by Snodgrass (1929), therein initially termed M. profurca-cervicalis transversalis (Ivlm10) (Fig. 28C), and runs from the profurcal arm to the cervical sclerite of the opposite body half. It is likewise found in all other examined representatives of the Acrididae (Misra 1946; Albrecht 1953), in Eumastacidae (Blackith & Blackith 1967), and Pyrgomorphidae (Maki 1938; Blackith & Blackith 1967). In *Cephalocoema* neither Ipcm2 nor Ivlm10 is present (de Zolessi 1968).



Muscle present in groundpattern of Orthoptera, Ensifera or Caelifera.
Groundpattern uncertain, muscle present in some Orthoptera, Ensifera or Caelifera.
Presence of muscle apomorphy of grylloid clade, Gryllidae, Tettigoniidae or Anostostomatidae.

As Ivlm10 is never described to be present simultaneously with Ipcm2, and both insert at the same point, it is likely that these muscles are homologous, albeit differing in the point of origin. Interestingly, among the investigated representatives of the Caelifera, the muscle Ipcm2 is solely found in *Xya*. This taxon is a representative of the pygmy mole crickets (Tridactylidae), a basal lineage of short-horned grasshoppers that has been recovered as sister taxon to the remaining Caelifera in a number of phylogenetic analyses (Flook *et al.* 1999; Zhang *et al.* 2013; Song *et al.* 2015). Hence, the presence of Ipcm2 in *Xya* might be supporting this hypothesis as a putative ground plan feature of all Orthoptera. If the replacement of Ipcm2 by Ivlm10 might represent an autapomorphy of the remaining Caelifera has to be elucidated by the investigation of additional caeliferan representatives.

Ipcm8 (M. propleuro-trochanteralis) is a muscle running from the propleura to the trochanter of the fore leg that is present in all polyneopteran taxa. Yet, its characteristics differ between Orthoptera and most Polyneoptera. In Polyneoptera it generally appears as a single muscle (e.g. Bharadwaj & Chadwick 1974a; Wipfler *et al.* 2015). In Orthoptera this muscle is composed at least of two bundles (Fig. 28A), with the exception of the gaudy grasshopper *Atractomorpha*, for which only a single muscle is described (Maki 1938). For the remaining Polyneoptera, a likewise two-bundled muscle Ipcm8 is only reported for *Periplaneta* (Carbonell 1947). Both bundles of Ipcm8 in *Periplaneta* originate from the pleural arm (Carbonell 1947). In all representatives of Caelifera, the respective muscle is consisting of a bundle originating from the undersurface of the pleural arm, in addition to a bundle that originates from the dorsal area of the episternum (e.g. Albrecht 1953; Blackith and Blackith 1967; de Zolessi 1968). Only in matchstick grasshoppers (Eumastacidae) (Blackith & Blackith 1967) and in *Xya* (Tridactylidae) (Supplementary Plate 45) an additional bundle of Ipcm8 is present that originates from the pleural ridge. All representatives of Ensifera are characterized by a two-bundled Ipcm8, whereby one bundle originates dorsally from the episternal area of the cryptopleura, the other from

Figure 28 (see opposite page). Thoracic musculature of Orthoptera. (A) Dorsal longitudinal and pleurocoxal muscles. (B) Sternocoxal muscles. Tergopleural muscles that are present in unwinged Orthoptera. (C) Ventral longitudinal, sternopleural and pleuropleural muscles.

the epimeral area or pleural ridge of the cryptopleura (e.g. Figs. 14B, 17A, 20A). This common feature of Ensifera was regarded as a potential autapomorphy for this group by Ander (1939). Nevertheless, the bundle of Ipcm8 that runs from the pleural arm found in Caelifera and the one in Ensifera originating from the epimeral area or pleural ridge might represent a homologous bundle since a pleural arm is generally lacking, being only present in the prothorax of Caelifera (e.g. Snodgrass 1929; Matsuda 1970).

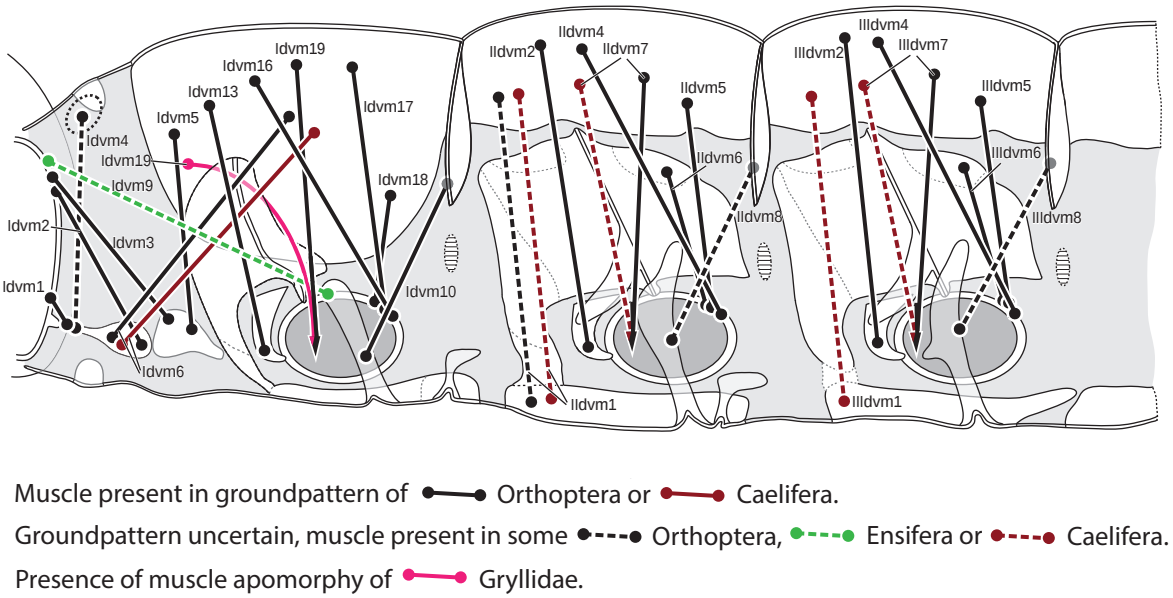


Figure 29. Dorsoventral musculature in the thorax of Orthoptera.

All neopteran insects are characterized by specific thoracic muscles that are related to the trochanter (Friedrich & Beutel 2008). These trochanteral muscles are composed of several bundles that originate from different parts of the thoracic skeleton running together in one tendon (Friedrich & Beutel 2008). Generally, three muscles are differentiated in the pterothorax: II/IIIdvm7 (Mm. noto-trochanteralis) running from the notum of a pterothoracic segment (Fig. 29), II/IIIpcm5 (Mm. episterno-trochanteralis) originating from the episternum (Fig. 28A) and II/IIIscm6 (Mm. furca-trochanteralis) running from the furcal arm to the trochanter (Fig. 28B). Interestingly, the Mm. episterno-trochanteralis of the pterothorax is solely present in members of the Ensifera (Fig. 28A). In contrast, a second bundle of the Mm. noto-trochanteralis is present in the pterothorax of Caelifera (Fig. 29) that

might represent the translocated bundle of the episternal muscle found in Ensifera. With the exception of *Cephalocoema* (Proscopiidae) (de Zolessi 1968), this second noto-trochanteral bundle is found in the remaining investigated caeliferan taxa (e.g. Snodgrass 1929; Misra 1947), and also in some further taxa that were not included in the present phylogenetic analyses (Maki 1938; Ewer 1958).

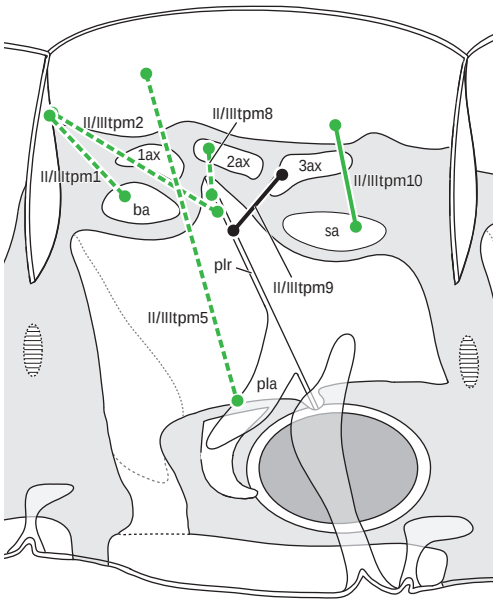


Figure 30. Tergopleural musculature in the pterothorax of winged Orthoptera. Abbreviations: *1/2/3ax* first/second/third axillary sclerite, *ba* basalare, *pla* pleural arm, *sa* subalare.

Some more worthwhile findings are related to the characteristics of the indirect flight musculature occurring in Caelifera and in Ensifera in particular. Orthoptera in general are considered to have a decreased flight ability and performance, since they primarily move by jumping (Beier 1972). The wings are mainly used to control the direction and trajectory during the jumping process (Beier 1972). While there is no support for ensiferan representatives having an enhanced flight ability (Ander 1939; Beier 1972), the only caeliferan taxa for which excellent and enduring flight abilities are reported are the swarming grasshoppers (e.g. *Schistocerca*, *Locusta*) (Beier 1972). Two muscles that are indirectly involved in flying are the Mm. pleura-sternalis (II/IIIspm1) and Mm. noto-sternalis (II/IIIdvm1) since they have a supporting function in spreading and raising the wings (Voss 1905b). Both of these muscles are present in the meso- as well as in the metathorax of only certain caeliferan taxa: in short-horned grasshoppers and locusts (Acrididae) (e.g. *Locusta*: Albrecht 1953; *Schistocerca*: Misra 1947), toad grasshoppers (Pamphagidae) (*Lamarckiana*: Thomas 1952), and gaudy grasshoppers (Pyrgomorphidae) (*Atractomorpha*: Maki 1938; *Zonocerus*: Ewer 1954). However, none of these muscles are developed in the pterothorax of the tridactylid *Xya* (this study), the proscopiid *Cephalocoema* (de Zolessi 1968), and the grasshopper

Lentula (Ewer 1958). The presence or absence of these muscles might be related to the occurrence of wings, since the aforementioned representatives are either completely wingless (*Cephalocoema* or *Lentula*) or at least brachypterous (*Xya*). This view is shared by Zechner *et al.* (1999) based on a study on *Xya pfaendleri*. In populations of this usually brachypterous tridactylid species fully winged specimens are regularly documented. In contrast to the brachypterous morphs, the fully winged specimens are reported to be good flyers and to have well developed flight musculature (Zechner *et al.* 1999).

In Ensifera, the occurrence of the muscles dvm1 and spm1 in the pterothorax is quite different from that of the Caelifera. Here, both muscles are exclusively developed in the mesothorax. Additionally, these indirect flight muscles are not present in all representatives of the Ensifera. The muscle IIdvm1 (M. mesonoto-sternalis) is present in Gryllidae (e.g. Voss 1905c, d; Carpentier 1923; Maki 1938), some representatives of the Tettigoniidae (*Tettigonia*: this study; *Conocephalus*: Maki 1938), and the prophalangopsid *Cyphoderris* (this study). To the contrary, the muscle IIspm1 (M. mesopleura-sternalis) is solely found in *Cyphoderris* (this study) and documented for some representatives of the Gryllidae (*Gryllus*: Carpentier 1923; *Acheta*: Voss 1905c; *Tarbinskiellus*: Maki 1938). Surprisingly, IIspm1 is not found in the specimen of *Gryllus* examined in the present study. The occurrence of IIspm1 might be related to the sex of the studied specimen as it is probably only present in males. Among my examined specimens only *Cyphoderris* (Prophalangopsidae) is a male. No author of past studies provides information on the sex of the examined species (e.g. Voss 1905a, b, c; Carpentier 1921; Carpentier 1923; Maki 1938). It is striking that IIspm1 as well as IIdvm1 are solely developed in ensiferan taxa that communicate by tegminal stridulation. However, both muscles are not directly involved in the process of sound production, since the horizontal movement is caused by the action of certain tergopleural muscles (Voss 1905b; Pfau & Koch 1994). Nonetheless it is plausible that the presence of both muscles in the mesothorax of stridulating ensiferans enables a more effective and coordinated tegminal movement. Additionally, at least the basalar muscle IIspm1 is reported to be involved in a warm-up phase before stridulation itself in regulating the body temperature (Heller 1986).

Phylogeny of Neoptera with special emphasis on the internal relationships of Orthoptera and Ensifera in particular

The evolution of wings is regarded as a key innovation for the evolutionary success of insects (Engel *et al.* 2013). The morphology of insect wings plays a substantial role for recognizing and describing taxa (Béthoux & Nel 2001; Béthoux 2005, 2007), represents a topic of comparative morphological studies (Hörnschemeyer 2002; Willkommen 2008) and provides numerous traits for phylogenetic analyses(Yoshizawa 2011; Wipfler *et al.* 2015). Still, secondary winglessness is a widespread phenomenon among pterygote insects (Roff 1994), causing severe problems for phylogenetic reconstructions due to a critical amount of missing data when winged taxa are analyzed together with winged species (Wipfler *et al.* 2015). In my current study, two data sets are analyzed, the first including characters of the wing including wing base (complete data set), the other excluding these characters (reduced data set). This allows to infer the effect of the presence or absence of this character system for the phylogenetic reconstruction of Polyneoptera, in which either whole subgroups are wingless, e.g. Mantophasmatodea and Gryloblattodea, or the amount of wingless taxa within groups is exceedingly high, e.g. Phasmatodea or Orthoptera. The analysis of thoracic characters including those of the wing and wing base in particular leads to a surprisingly well resolved tree (Fig. 25). Nonetheless, the basal nodes mainly gain support by wing and wing base characters with a poor decay index or bremer support (Bremer 1994) leading to a polytomy in the analysis of the reduced data set/excluding those characters.

The relationships of the three major neopteran lineages, Holometabola, Paraneoptera (lice, cicadas, thrips and true bugs) and Polyneoptera, have been a constantly debated issue in insect phylogenetics (Ishiwata *et al.* 2011; Yeates *et al.* 2012; Sasaki *et al.* 2013; Letsch & Simon 2013; Simon & Hadrys 2013; Misof *et al.* 2014). Whereas the monophyly of Holometabola was not seriously questioned in the past (Beutel *et al.* 2011), a number of contradicting hypotheses on paraneopteran and polyneopteran relationships exist. Paraneoptera are either thought to have a single origin (Yoshizawa & Saigusa 2001; Kjer *et al.* 2006; Letsch & Simon 2013) or to be paraphyletic, with a closer relationship of bark and true lice (Psocodea) to Holometabola (Ishiwata *et al.* 2011; Misof *et al.* 2014). Herein, the monophyly of Holometabola is supported by several characters which were

already presented before (Friedrich & Beutel 2010; Wipfler *et al.* 2015). Also Paraneoptera are found to be monophyletic showing similarities in the morphology of the wing base (humeral plate and dorsal basisubcostale fused, a dorsally swollen second axillary, and an articulation between basalare and basisubcostale) confirming some of the derived characters proposed by Yoshizawa & Saigusa (2001). However, a closer relationship of Holometabola and Paraneoptera (= Eumetabola) is not supported by the current phylogenetic analysis, instead Paranoptera forms a sister to Polyneoptera. However, this relationship is only supported by a few ambiguous characters (profurca and propleura connected by muscle, prospina present, and posterior notal wing process fused to notum). Hence, this hypothesis might be a result of the limited taxon sampling of Paraneoptera as only two representative species are included in the analysis.

Revealing the evolution and internal relationships of Polyneoptera, or "Lower Neoptera", is a longstanding challenge in entomological research (Beutel *et al.* 2013). Only the most recent phylogenetic studies based on molecular (Ishiwata *et al.* 2011; Sasaki *et al.* 2013; Letsch & Simon 2013; Misof *et al.* 2014; Song *et al.* 2016) and morphological data (Yoshizawa 2011; Wipfler *et al.* 2015) confirm monophyletic Polyneoptera. Nevertheless, the morphological characters supporting their single origin are sparse and mainly concern structures found in the wing base and wing morphology itself (Wipfler *et al.* 2015). Not surprisingly, the monophyly of Polyneoptera could only be confirmed in the analysis including characters of the wing. The majority of autapomorphies of Polyneoptera coincide with those found by Wipfler *et al.* (2015), e.g. the presence of dorsal cervical sclerites, a prothoracic anapleural ridge, and the muscle IIscm3 that connects the mesofurcal arm to the mesal mesocoxal rim. Nonetheless, the obtained characters representing ground plan features of the wing in Polyneoptera show some differences between the present study and the study of Wipfler *et al.* (2015). In contrast to Wipfler *et al.* (2015), all derived characters proposed by Yoshizawa (2011) are confirmed to be apomorphies of Polyneoptera: a dorsally membranous humeral plate, a side-by-side articulation of the median notal wing process and the body of the first axillary, a long proximal tail of the body of the first axillary that articulates with the median notal wing process along long margins, and an at-point articulation between basalare and humeral plate. A distinctly enlarged hind wing vannus, a potential synapomorphy of Polyneoptera (Kristensen 1991; Klass 2007), is only confirmed under accelerated transformation (ACCTRAN)

assumption which prefers an earlier origin and given the same number of steps on the tree. As in Wipfler *et al.* (2015), the presence of a side-by-side articulation between the antemedian notal wing process and the first axillary sclerite is found as an additional character supporting the monophyly of Polyneoptera. Nonetheless, this result might be related to the limited taxon sampling, since this side-by-side articulation is also found in scorpion flies (Mecoptera) (Yoshizawa 2011). Given the assumption that this character is homologous in all taxa it could thereby likewise represent a plesiomorphy for Polyneoptera. In the present study, two further characters are found to be apomorphic/derived for Polyneoptera: the presence of muscle IIdvm2 that connects the mesonotum with the mesothoracic trochantin (with a reversal in *Comicus* and *Troglophilus*), and the presence of IIIscm3 that connects the metafurcal arm with the mesal metacoxal rim (? for Blattodea and *Schizodactylus*).

Only in the complete analysis a satisfactory resolution could be achieved regarding the internal relationships of Polyneoptera (Fig. 25). Based on this data set the previously hypothesized sister group relationship of stoneflies (Plecoptera) and the remaining taxa of Polyneoptera (= Pliconeoptera) (Wipfler *et al.* 2015) is confirmed. In accordance to the study of Wipfler *et al.* (2015), this hypothesis is supported by several homoplasious characters, e.g. two pairs of lateral cervical sclerites present (also present in Neuroptera and Psocoptera; character change to a single pair of cervical sclerites in Ensifera, reversal to paired cervical sclerites in Schizodactylidae) and the mesospina situated on a distinct spinasternite (reversal in Mantophasmatodea and Orthoptera where the mesospina is situated on posterior part of the basisternite). Within the Pliconeoptera, several taxa are recovered as monophyletic, e.g. stick and leaf insects (Phasmatodea), ice crawlers + heel walkers (Xenonomia), praying mantises + cockroaches (Dictyoptera), and grasshoppers, katydids and relatives (Orthoptera). The phylogenetic affinities of webspinners (Embioptera) were repeatedly debated in the past. Evidence for a sister group relationship with Phasmatodea (together Eukinolabia) is strongly provided by molecular data (Terry & Whiting 2005; Sasaki *et al.* 2013; Letsch & Simon 2013; Misof *et al.* 2014). Eukinolabia is also supported by several morphological characters occurring in both subtaxa like an additional head muscle and the structure of the eggs bearing an operculum and a micropylar plate (Rähle 1970; Tilgner 2002; Bradler 2009). Based on other morphological characters like the reduced cerci and tarsomeres, other authors favor a sister group relationship

of Embioptera to Zoraptera (=Mystroptera) (Kristensen 1991; Engel & Grimaldi 2000; Rafael & Engel 2006). Yoshizawa (2011) also found strong support of a clade Mystroptera based on characters of the wing base. As the complete data set includes characters previously analyzed by Yoshizawa (2011), I also found support for the clade Mystroptera. All apomorphies of Mystroptera hypothesized by Yoshizawa (2011) are confirmed by the analysis of the complete data set: a strongly sclerotized tegula, a basal hinge between notum and posterior notal wing process, and an enlarged head of the first axillary. A closer relationship of Phasmatodea, Dictyoptera, Xenonomia, and Orthoptera is only weakly supported by several ambiguous characters. Nonetheless, one has to pay special attention to a character describing the invagination point of the pleural arm in the meso- and the metathorax: the pterothoracic pleural arms in Phasmatodea, Dictyoptera and Orthoptera are situated ventrad in direct proximity to the pleural condylus. In Xenonomia, the pleural arm is located posterior to the pleural ridge forming an internal process of the epimeron, which represents a unique feature of these insects (Wipfler *et al.* 2015). Interestingly, also this processus is situated in the lower, more ventral part of the epimeron (Walker 1938; Wipfler *et al.* 2015). In all other examined taxa with a prominent pleural arm in the meso- and metathorax it invaginates near the middle or in the dorsal area of the pleural ridge. In Embioptera, like in the phasmid *Timema*, no distinct pleural arm is developed (Bharadwaj & Chadwick 1974b; Klug 2008). Therefore, the respective character was coded as not applicable for both taxa. Nevertheless, the muscle connecting the furcal arm with the respective pleural arm, M. furca-pleuralis (II/IIIspm2), inserts near the pleural condylus in both taxa (Klug 2008). Hence, this characteristic gives support for including Embioptera in a clade also comprising Dictyoptera, Phasmatodea, Orthoptera and Xenonomia. This characters migh thereof serve as an supporting argument for a single origin of a clade comprising Orthoptera, Xenonomia, Dictyoptera, Phasmatodea + Embioptera, a clade that also finds strong support in the most recent phylogenomic study of insects (Misof *et al.* 2014).

The position of Orthoptera within Polyneoptera still remains a matter of debate. Recent cladistic studies including representatives of the Xenonomia (heel walkers + ice crawlers) either propose a closer relationship of Orthoptera to Phasmatodea (Beutel & Gorb 2006; Yoshizawa 2011), a sister group relationship to Phasmatodea + Embioptera (Terry & Whiting 2005), or to Dictyoptera + Zoraptera (Ishiwata *et al.* 2011; Sasaki *et al.* 2013).

In others, Orthoptera forms the sister to a clade comprising Xenonomia, Embioptera, Phasmatodea and Dictyoptera (Misof *et al.* 2014), or to Xenonomia, Embioptera, Zoraptera, Phasmatodea and Dictyoptera (Song *et al.* 2016). Walker (1938) who examined the thoracic morphology of *Grylloblatta* assumed a close relationship of Grylloblattodea to his 'Orthopteroida' (including Dictyoptera, Orthoptera and Phasmatodea). Beier (1972) includes the Notoptera (= Grylloblattodea) into his taxon 'Saltatoria' proposing a close relationship of Grylloblattodea to short-horned (Caelifera) and long-horned grasshoppers (Ensifera). In both of the present analyses, Xenonomia are found to be the sister group of Orthoptera. This relationship is only weakly supported by homoplasious characters: a pronotum that is laterally partly or completely connected with the propleura (also present in Embioptera, *Timema*, and Psocoptera), the absence of muscle IIscm2 that connects the mesofurca with the posterior mesocoxa (? in *Schizodactylus*, *Acheta* and Hymenoptera), and the secondary absence of muscle IIIdvm3 that connects the central area of the metanotum with the metathoracic trochantin (? in Mantophasmatodea and *Schizodactylus*).

The main focus of the present study lies on the phylogenetic affinities and internal relationships of the Orthoptera. It is remarkable that the reconstructed branching pattern of Orthoptera is nearly congruent in both of the analyses. This indicates that the herein examined characters of the wing and wing base are not relevant to reconstruct the internal relationships of the Orthoptera. As in Wipfler *et al.* (2015), the monophyly of Orthoptera is strongly supported, but some additional, mainly unambiguous autapomorphies are recovered: connection of propleura and prosternum as pleurosternal bridge (in convergence to Mantodea), pterothoracic furcae enclosing the respective pleural arm from the ventral side, mesospina and mesofurcae situated in one line on sternacosta, and a stalked mesospina with distal plate and/or processi. In accordance to the majority of phylogenetic studies, the short-horned grasshoppers (Caelifera), as well as the long-horned grasshoppers (Ensifera), are found to form monophyletic subtaxa of the Orthoptera (Flook *et al.* 1999; Zhang *et al.* 2013; Song *et al.* 2015). The monophyly of Caelifera is strongly supported by a number of characters, e.g. the presence of an anterior mesofurcal processus (also present in Mantophasmatodea, Psocoptera, and Neuroptera), the absence of the muscles IIpcm5 (also absent in Thysanoptera and

Neuroptera) and IIIpcm5 (also absent in *Megacrania* and Holometabola), and the presence of a duplicated Idvm6. A sister group relationship of stick grasshoppers (Proscopiidae) and matchstick grasshoppers (Eumastacidae), hypothesized in the most comprehensive molecular orthopteran phylogeny to date (Song *et al.* 2015), is also confirmed in the present analysis. Astonishingly, a closer relationship of the pygmy mole cricket *Xya* to the Acrididae is recovered in the analysis of the complete data set, a result conflicting with current hypotheses, according to which the Tridactylidae always forms the sister to all remaining Caelifera (Flook *et al.* 1999; Zhang *et al.* 2013; Song *et al.* 2015). However, my contradicting novel hypothesis is only supported by a single, ambiguous synapomorphy: the absence of muscle IIdvm8. Since this muscle is also frequently absent in distantly related taxa (Ephemeroptera, Neuroptera, Mantophasmatodea and some taxa within Ensifera), its absence in Tridactylidae and Acrididae might as well represent an artifact of the limited taxon sampling in regard of Caelifera. Furthermore, there are some morphological characteristics of Tridactylidae that are plesiomorphic among caeliferans and support their basal placement within Caelifera: the presence of muscle Ipcm2 often found in Ensifera but absent in all remaining Caelifera and the spatulate form of the lateral metafurcal arm also found in Gryllidae, Gryllotalpidae and Gryllacrididae.

Based on the morphology of the thorax, the phylogenetic relationships within the Ensifera appear fairly well resolved, although only weakly supported (Fig. 25). The monophyly of Ensifera is supported by the secondary presence of a single lateral cervical sclerite (with one reversal in Schizodactylidae) and the presence of the muscle IIppm1 that connects distant parts of the pleura (also present in Neuroptera, Plecoptera, and the stick insect *Megacrania*). Ensifera are found to be divided into two major lineages: grylloid clade (crickets and mole crickets) and tettigonioid clade (katydids and allies). Originally hypothesized by Ander (1939), albeit based on an informal analysis of different morphological character complexes, this basal branching pattern is confirmed by more recent cladistic analyses of morphological (Desutter-Grandcolas 2003) and molecular data (Song *et al.* 2015). All examined representatives of the grylloid clade share two unambiguous apomorphies: the presence of muscle Itpm2-2 that connects the occipital rim to the anterior edge of the cryptopleura and an unpaired muscle Ivlm8. Also the two examined representatives of the true crickets, *Acheta* and *Gryllus*, form a monophyletic group, supported by several characters such as a paired and freestanding prothoracic

furcasternite and a muscle ldvm19 with two bundles whose anterior one is running behind the cryptopleura. According to recent comprehensive phylogenetic studies the grylloid clade consists of two main lineages, the Gryllotalpoidea and the Grylloidea (Song *et al.* 2015; Chintauan-Marquier *et al.* 2016). The Gryllotalpoidea comprises at least mole crickets (Gryllotalpidae) and ant-loving crickets (Myrmecophilidae). Grylloidea on the other hand comprises apart from true crickets other diverse taxa such as Phalangopsidae (spider crickets) and Trigonidiidae (ground crickets and trigs). Scaly crickets (Mogoplistidae) either belong to Gryllotalpoidea (Song *et al.* 2015) or to Grylloidea (Chintauan-Marquier *et al.* 2016). To further validate the aforementioned characters as synapomorphies for the whole grylloid clade or the Grylloidea respectively, more representatives of this species-rich and taxonomically diverse group need to be examined. Until now, especially the limited taxon sampling of Grylloidea might lead to misguided assumptions regarding the specific characters found in *Acheta* and *Gryllus*. For instance the prothoracic furcasternite of *Phaeophilacris bredoides*, a cave-dwelling representative of the Grylloidea belonging to the Phalangopsidae, is not a freestanding paired sclerite but fused with the basisternite as in all other examined ensiferans (*pers. observ.*). A paired free-standing profurcasternite might thereby represent an autapomorphy of a more restricted subgroup of Grylloidea, perhaps the Gryllidae (*sensu* Chintauan-Marquier *et al.* 2016).

The herein reconstructed internal relationships of the tettigonioid clade represent a novel hypothesis. Katydids and bush-crickets (Tettigoniidae) form an independent lineage from all remaining tettigonioid groups which include raspy crickets (Gryllacrididae), dune crickets (Schizodactylidae), Jerusalem crickets (Stenopelmatidae), king crickets and weta (Anostostomatidae), cave crickets (Rhaphidophoridae), and hump-winged crickets (Prophalangopsidae) (Fig. 25). This clade is supported by a posterior profurcal branch appearing as an arm-like tapered process (also present in *Gryllotalpa*), a paired posterior processus of the stalked prospina (reversal in Prophalangopsidae), and the presence of muscle IIIspm5 (also present in Mantophasmatodea; reversal in Stenopelmatidae).

The most surprising finding is the phylogenetic position of the Prophalangopsidae as sister group to Rhaphidophoridae within a clade also comprising Anostostomatidae, Stenopelmatidae and Schizodactylidae. The species-poor Prophalangopsidae, the only extant members of the group Hagloidea (or Haglidae), was previously thought to form the sister group of the Tettigoniidae because of their strikingly similar mode of tegminal

stridulation that involves nearly identical structures (Zeuner 1939; Ragge 1955; Gwynne 1995; Desutter-Grandcolas 2003). However, in accordance to the findings of the present analysis, recent molecular phylogenetic studies propose a closer relationship of Prophalangopsidae to Rhaphidophoridae (Zhou *et al.* 2014) or to Anostostomatidae, Gryllacrididae and Stenopelmatidae (Legendre *et al.* 2010; Song *et al.* 2015). An unambiguous autapomorphy supporting the monophyly of a clade comprising Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae and Anostostomatidae is the triramous metafurca bearing a lateral, an anterior and an additional dorsal processus. A triramous metafurca is likewise reported for additional representatives of the Anostostomatidae, *Anabropsis* sp. (Naskrecki 2000) and another species of *Hemideina* (Maskell 1927), and Rhaphidophoridae, namely *Diestrammena* (Carpentier 1921a, 1923), *Ceuthophilus* (Gurney 1935), and *Macropathus* (Richards 1955). This further strengthens the assumption that this trait is an autapomorphy of this clade.

The phylogenetic position of dune crickets (Schizodactylidae), a relict group of psammophilous ensiferans, was repeatedly questioned in the past. Taxonomic and cladistic studies either favor a closer relationship of Schizodactylidae to the grylloid clade (Gwynne 1995; Legendre *et al.* 2010), or a grouping next to or within the tettigonioid clade (Ander 1939; Gorochov 1995a, 2001; Desutter-Grandcolas 2003; Song *et al.* 2015). In the present analysis, Schizodactylidae forms the sister group to a clade comprising Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae. Morphological characters that support this whole lineage are the secondary presence of a freestanding profurca that is not in contact with the propleura (reversal in Anostostomatidae: here profurca and propleura are connected by muscle Ispm1), the secondary presence of an arm-like lateral metafurcal process, and the presence of muscle Idvm9 (also present in Archostemata, Hymenoptera, and Meconematinae).

Evolution of communication in extant Ensifera

Ensiferans are renowned for their intraspecific social communication by airborne sounds. Especially signals produced by the rapid friction of the forewings (tegminal stridulation) are well known from the subgroups Gryllidae, Gryllotalpidae, Tettigoniidae, and Prophalangopsidae (Beier 1972; Otte 1992). These airborne sounds are detected by

an auditory chordotonal organ in the tibia of the foreleg, the tibial organ, in association with a thin membrane, the tibial tympanum (Yager 1999; Strauß *et al.* 2014b). Several morphological traits (the stridulatory file, resonating and amplifying areas of the wing, tympanal anatomy, acoustic tracheae) as well as behavioural aspects (female phonotaxis, structure and performance of calling songs) disclose tegminal stridulation to be one of the most complex acoustical mechanisms among insects (Jost & Shaw 2006). However, tegminal stridulation as a form of acoustic communication does not alone represent the diversity of acoustic structures, interactions, and behaviours within the Ensifera (Desutter-Grandcolas 2003). According to Desutter-Grandcolas (2003), at least the femoro-abdominal stridulatory apparatus that is present for instance in king crickets and wetas (Field 2001) or raspy crickets (Rentz 1996) should be taken into account when discussing the evolution of acoustic communication within the Ensifera. Table 4 compiles literature information of all major ensiferan lineages on the structure and anatomy of their tibial organs, modes of acoustic communication, and the context in which they are used. Acoustic signals in general may be used in two differing contexts. The emitted sound may function as a signal for an individual of a different species, e.g. defending and deterring a predator, termed interspecific communication (Desutter-Grandcolas 2003). In contrast, the emitted sound may target conspecifics, e.g. in defence or rivalry against other males or to attract females, termed intraspecific communication (Desutter-Grandcolas 2003). Whereas tegminal stridulation is mainly used an intraspecific context (Otte 1992; Greenfield 1997; Desutter-Grandcolas 1997; Howard & Hill 2006), the communication with conspecifics by femoro-abdominal stridulation tend to be the exception (Field 2001).

Tegminal stridulation and tibial organs among Ensifera are frequently regarded as too similar and too complex structures to have evolved more than once (Alexander 1962; Otte 1992). In contrast, based on phylogenetic considerations under the parsimony criterion, the more parsimonious and thus favoured explanation suggests an ensiferan ancestor lacking stridulatory and auditory structures, and that tegminal stridulation as well as tympanal organs evolved several times independently within Ensifera (Ander 1939; Gwynne 1995; Desutter-Grandcolas 2003). To elucidate these two contradicting evolutionary scenarios, the occurrence of tegminal stridulation, femoro-abdominal stridulation, and that of tympana in the forelegs is traced based on the novel hypothesis on phylo-

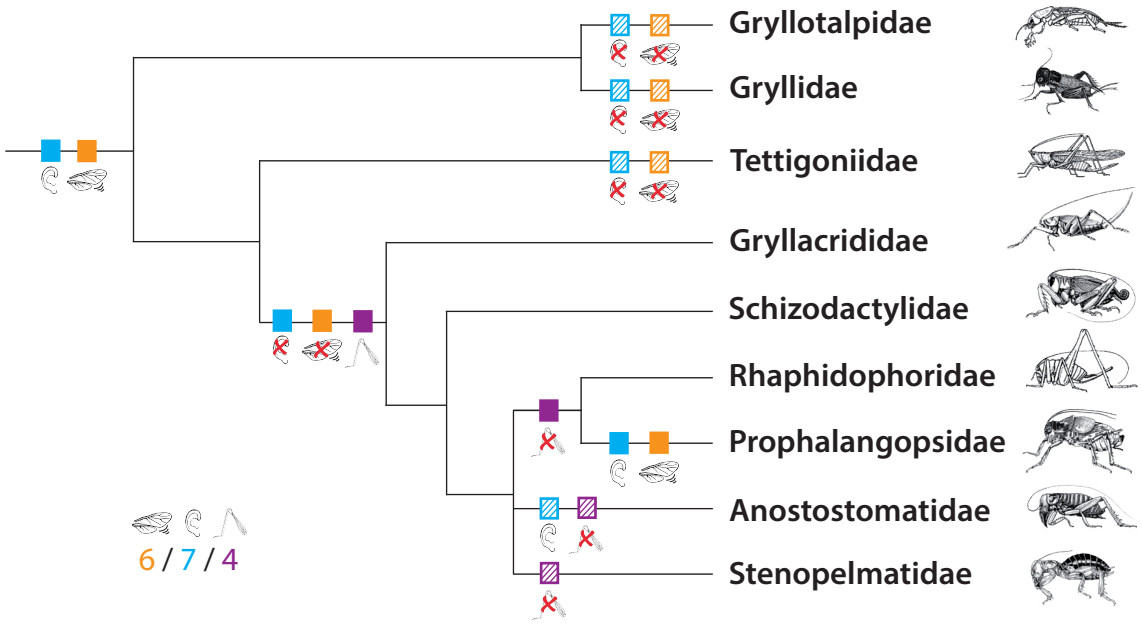
genetic relationships of Ensifera as proposed in the present study (Fig. 31). Interestingly, both hypotheses require the same amount of character changes (steps) on the reconstructed trees, thereof being equally probable by means of cladistic's parsimony principle. This raises the question which of these scenarios is more plausible in the evolutionary context.

Single or convergent origin of tibial tympana and tegminal stridulation?

In the first scenario it is assumed that the last common ancestor of Ensifera was capable of emitting airborne sounds by tegminal stridulation and of hearing those sounds by a fully functional tibial organ with a prominent tympanum. Consequently, in the last common ancestor of the clade comprising Gryllacrididae, Schizodactylidae, Rhaphidophoridae, Prophalangopsidae, Anostostomatidae, and Stenopelmatidae both abilities were lost, since the majority of those taxa is silent and deaf. In consequence, tegminal stridulation and tympana must have evolved secondarily in Prophalangopsidae. Indeed, there is some evidence that tegminal stridulation in Prophalangopsidae is not perfectly adapted for intraspecific communication. Interestingly, the hearing sensitivity of the tibial organ of *Cyphoderris* species mismatches with the frequency emitted by their "calling songs" (Mason 1991). However, Mason (1991) only examined the tympanal organ of male individuals and assumes a comparable sensitivity in females, although sexual differences in the sensitivity of tibial organs are known from few katydid species (Bailey & Römer 1991; Bailey & Kamien 2001). Nonetheless, positive phonotaxis of female *Cyphoderris* was never observed in the field (Morris *et al.* 2002). The sound signals of male *Cyphoderris* might not primarily be used to attract females from long distances, but rather play a role in male-male-interactions and territoriality (Mason 1996). Nevertheless, the loss of tympana and tegminal stridulation in the last common ancestor of the clade comprising Gryllacrididae, Schizodactylidae, Rhaphidophoridae, Prophalangopsidae, Anostostomatidae, and Stenopelmatidae appears not plausible in an evolutionary context. Why should a species loose the obviously advantageous ability to interact with conspecifics by a versatile and efficient acoustic communication system? The loss of tegminal stridulation and tympana might represent a consequence of wing and flight loss that is fairly common in the aforementioned taxa. A comparable correlation between the reduction of tympana, the loss of intraspecific communication and the loss of wings

What if...

...tympanal hearing and tegminal stridulation is ancestral in Ensifera?



...tympanal hearing and tegminal stridulation have convergent origins?

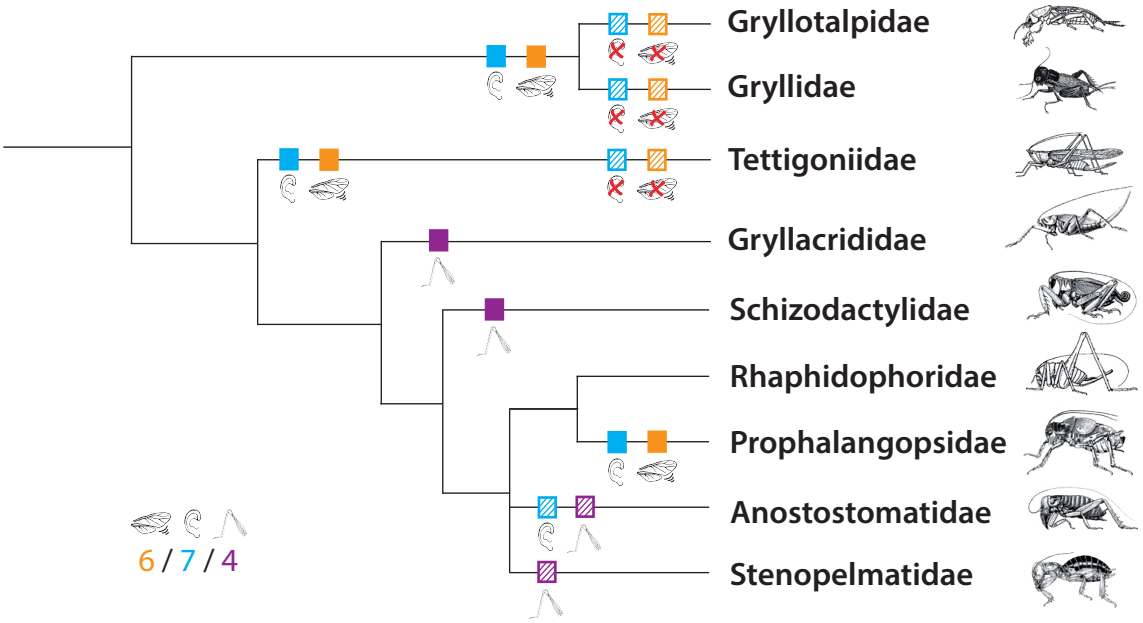


Figure 31. Tracing characters related to communication within the Ensifera. Two hypotheses are compared: changes assigned as close to the root as possible (ACCTRAN) and changes assigned as close to the tips as possible (DELTRAN). Both hypotheses are equally parsimonious. Characters: tympana in the tibia of the foreleg, tegminal stridulation and femoro-abdominal stridulation. Filled rectangles represent apomorphies for a taxon, hatched rectangles indicate a character change within the respective taxon.

and flight is documented for several other insect taxa (Otte 1990; Strauß & Stumpner 2015). The presence of tegminal stridulation and tympana is thought to be ancestral for crickets (Otte 1992; Desutter-Grandcolas 1997) and bush-crickets (Greenfield 1997; Naskrecki 2000). This directly allows to infer the mechanisms and consequences of the secondary loss of these structures in both taxa. Among Tettigoniidae the secondary loss of the tegminal stridulatory apparatus occurs only in very rare cases, for instance in certain genera (e.g. *Meconema*) or subordinate lineages, like stick katydids (Phasmodinae) or giant katydids (Phyllophorinae) (Ander 1939; Gwynne 1995). In other tettigoniids, at least the male has micropterous or brachypterous wings with an intact stridulatory apparatus, whereby the mechanism of intraspecific communication is still preserved in those taxa (Beier 1972; Rentz 2010). The tympanum of Tettigoniidae is present in virtually all taxa, even in wingless ones and in those that have no acoustic intraspecific communication (Sismondo 1980; Lehmann *et al.* 2007). Only the genus *Phasmodes* secondarily lacks tibial tympana, although vestiges are clearly visible (Lakes-Harlan *et al.* 1991; Naskrecki 2000). In a survey of Australian crickets, Otte (1990) clearly demonstrates that the presence of tegminal stridulation in crickets is always accompanied by the presence of a tympanum in both long-winged (and airworthy) or short-winged (and flightless) species. In contrast, crickets that lost the ability to stridulate always retain the tympanum if they are able to fly (Otte 1992). The frequently preserved acoustical hearing ability by functional tympana after the loss of intraspecific communication in Tettigoniidae and Gryllidae is likely caused by the necessity to deect potential predators (Otte 1990; Bailey 1993; Strauß & Stumpner 2015). The concurrent reduction of both tegminal stridulation and tibial tympana in Tettigoniidae as well as Gryllidae is rather uncommon in both taxa, but occurs more frequently in Gryllidae than in Tettigoniidae (Otte 1990; Bailey 1993). In contrast to the exeptional cases found in Tettigoniidae and Gryllidae, the vast majority of the remaining tettigonioid ensiferans are characterized by the absence of tegminal stridulation and also other acoustic intraspecific communicational modes and the co-occurring absence of tympana (Gorochov 2001). As stated above, the only other tettigonioid taxon apart from Tettigoniidae performing tegminal stridulation is Prophalangopsidae. Also tympana are rarely present in the clade comprising Gryllacrididae, Schizodactylidae, Rhaphidophoridae, Stenopelmatidae, Prophalangopsidae and Anostostomatidae. They are developed only in certain genera of the Anostostomatidae (Ball & Field 1981; Stringer 2006; Brettschneider

Table 4. Literature data on the presence/absence of tympana, the morphology of the tibial organ, and the different forms of communication found in all major taxa of Ensifera.

		intraspecific acoustic communication		interspecific acoustic communication	
	tympana in the foreleg and structure of the tibial organ	male-female interaction (calling, mating, courtship)	male-male interaction (courtship, aggression, defence)	defence, aggression	remarks
Rhaphidophoridae (cave crickets, cave wetas) 	tympana not present (Hubbell & Norton 1978; Stritih & Čokl 2012) tibial organ: subgenual organ (SGO), intermediate organ (IO) (*Troglophilus*: Strauß *et al.* 2014b)	 drumming on substrate (Tinkham & Rentz 1969; Weissmann 2001)	no acoustic communication in male-male interactions (Weissmann 1997)	no interspecific acoustic communication (Weissmann 1997; Desutter-Grandcolas 2003)	femoro-abdominal stridulatory apparatus not developed (*contra* Desutter-Grandcolas 2003)
Schizodactylidae (dune crickets) 	tympana not present (Strauß & Lakes-Harlan 2010) tibial organ: SGO, IO, crista acustica homologue (CAH) (*Comicus*: Strauß & Lakes-Harlan 2010)	?	?	?  femoro-abdominal stridulatory apparatus present in both sexes (Khattar 1972; Irish 1986); context of usage unknown (Strauß & Lakes-Harlan 2010)	elytro-femoral stridulatory mechanism in adults of fully winged species of *Schizodactylus*; context of usage unknown (Mason 1961)
Gryllacrididae (raspy crickets) 	tympana not present (Field & Bailey 1997; Strauß *et al.* 2014b) tibial organ: SGO, IO, CAH (*Ametrus*: Strauß & Lakes-Harlan 2008a)	 drumming on substrate (Hale & Rentz 2001)	?	 femoro-abdominal stridulation: forelegs raised and extended, only hindlegs (not abdomen) moving (Field & Bailey 1997)	femoro-abdominal stridulatory apparatus developed in all species, eponymic character of this taxon (Rentz 1996)

Table 4. Literature data on the presence/absence of tympana, the morphology of the tibial organ, and the different forms of communication found in all major taxa of Ensifera. *(continued)*

		intraspecific acoustic communication		interspecific acoustic communication	
	tympana in the foreleg and structure of the tibial organ	male-female interaction (calling, mating, courtship)	male-male interaction (courtship, aggression, defence)	defence, aggression	remarks
Anostostomatidae (king crickets, wetas) 	tympana not present, e.g. in *Hemiandrus* (Gwynne 2004), *Cnemotettix* (Caudell 1916), *Onosandrus*, and *Bochus* (Brettschneider *et al.* 2007) tympana present, e.g. in *Motuweta* (Johns 1997), *Exogryllacris* (Willemse 1963), *Hydolutus* (Derka & Fedor 2010), *Anisoura* (Ander 1933) tibial organ: SGO, IO, crista acustia (CA) (only described for tympanate genus *Hemideina*: Nishino & Field 2003)	 drumming on substrate reported for atympanate taxa (*Cnemotettix*: Weissmann 2001; *Hemiandrus*: Gwynne 2004  femoro-abdominal stridulation in tree and giant weta (*Hemideina* and *Deinacrida*: Field 1993a)	femoro-abdominal stridulation: only abdomen moving, inter-male competition (*Deinacrida* and *Hemideina*: Field 1993a,b; *Libanasidus*: Bateman and Toms 1998) mandibular stridulation e.g. in tusked weta (*Motuweta*: Field 1993b)	 femoro-abdominal stridulation: hindlegs raised and extended, only hindlegs (not abdomen) moving (Field 1993a), also present in atympanate taxa (*Hemiandrus*: Gwynne 2004)	in winged genera *Cratomelus* and *Leiomelus* both, tympana and femoro-abdominal stridulatory apparatus, not developed (Gorochov 2001) *Cratomelus* with rudimentary tegminal stridulatory apparatus (Ander 1939) or tegmino-alary stridulatory apparatus (Gorochov 2001)
Stenopelmatidae (Jerusalem crickets) 	tympana not present (Strauß *et al.* 2014b) tibial organ: SGO, IO, CAH (*Stenopelmatus*: (Strauß & Lakes-Harlan 2008b)	 drumming on substrate with abdomen (Weissmann 2001)	? sex clarification drums (SCD) only if SCD of male is answered by male (Weissmann 2001)	 femoro-abdominal stridulation: moving abdomen past hind femora or moving hind femora past stationary abdomen (Weissmann 2001)	interspecific femoro-abdominal stridulation present only in a single subgroup of Stenopelmatidae (Siinae: Gorochov 2001)

Table 4. Literature data on the presence/absence of tympana, the morphology of the tibial organ, and the different forms of communication found in all major taxa of Ensifera. *(continued)*

		intraspecific acoustic communication		interspecific acoustic communication	
	tympana in the foreleg and structure of the tibial organ	male-female interaction (calling, mating, courtship)	male-male interaction (courtship, aggression, defence)	defence, aggression	remarks
Haglidae (hump-winged crickets) 	tympana present (Gorochov, 2003) tibial organ: SGO, IO, CA (*Cyphoderris*: Mason 1991)	 tegminal stridulation for calling (Morris & Gwynne 1978; Mason 1991) ? switch-wing singing during courtship (Morris *et al.* 2002)	defence: "defensive stridulatory behaviour" (Field & Bailey 1997) aggression: overt against other males in *Cyphoderris monstrosa* (Mason 1996), not present in *C. buckelli* and *stepsiptans*: (Morris *et al.* 2002)	? Ander's organ: metanoto-abdominal stridulatory organ (teeth on metanotum, ridges on first abdominal tergite) (Ander 1938)	Hearing organ of *Cyphoderris* sensitive to airborne sound at low frequencies, not perfectly tuned for the species' calling song frequency (Mason 1991)
Tettigoniidae (katydids, bushcrickets) 	tympana present (Strauß *et al.* 2014b) rarily not present, e.g. in *Phasmodes* (Lakes-Harlan *et al.* 1991) tibial organ: SGO, IO, CA (Strauß *et al.* 2016); also in atympanate genus *Phasmodes* (Lakes-Harlan *et al.* 1991)	 tegminal stridulation (Greenfield 1997; Gwynne 2001)  hindleg drumming (*Meconema*: Sismondo 1980) tremulation (Morris *et al.* 1994)	tegminal stridulation (Simmons 1986)	 Tegminal stridulation known from few isolated cases (Pfau 1988; Belwood 1990) stridulation of hind wings against modified abdominal tergites (*Mygalopsis*: Sandow & Bailey 1978; *Pantecphylus*: Heller 1996) mandibular-labral stridulation (*Sexava*: Lloyd & Gurney 1975) further examples of defensive acoustic stridulation in Heller 1996	tegminal stridulation and presence of tympana ancestral (Naskrecki 2000; Desutter-Grandcolas 2003)

Table 4. Literature data on the presence/absence of tympana, the morphology of the tibial organ, and the different forms of communication found in all major taxa of Ensifera. *(continued)*

		intraspecific acoustic communication		interspecific acoustic communication	
	tympana in the foreleg and structure of the tibial organ	male-female interaction (calling, mating, courtship)	male-male interaction (courtship, aggression, defence)	defence, aggression	remarks
Gryllidae (true crickets and allies) 	tympana present (Michel, 1974; Strauß *et al.* 2014b) not present in some genera/species e.g. in *Phaeophilacris* (Lunichkin *et al.* 2016), and entire lineages e.g. Myrmecophilinae, ant-loving crickets (Otte 1990) tibial organ: SGO, tympanal organ (TO) (Strauß *et al.* 2014b); structure similar in atympanate genus *Phaeophilacris* (Michel 1980)	 tegminal stridulation (Otte 1992; Desutter-Grandcolas 1997)  foreleg drumming (Phalangopsidae: de Mello & dos Reis 1994) wing-flicks (in atympanate genus *Phaeophilacris*: Dambach & Lichtenstein 1978)	tegminal stridulation (Otte 1992)	no acoustic communication in interspecific context (Otte 1992)	tegminal stridulation and presence of tympana ancestral; several losses within the group (Alexander 1962; Otte 1992)
Gryllotalpidae (mole crickets) 	present (Hill *et al.* 2002; Howard *et al.* 2008) absent in mute genus *Triamescaptor* (Hill *et al.* 2002) tibial organ: SGO, TO (*Gryllotalpa*: (Strauß *et al.* 2014b)	 tegminal stridulation (Howard & Hill 2006)	? no acoustic male-male interaction during calling season males form isolated acoustic chambers in "lek-like arenas" (Hill 1999)	?	tegminal stridulation and presence of tympana ancestral (Hill *et al.* 2002)

et al. 2007) and in Prophalangopsidae (Ander 1939; Mason 1991). These findings gather first hints arguing for a convergent origin of both tegminal stridulation and tympana within the Ensifera. In the following further arguments for this hypothesis are elucidated.

Arguments for the hypothesis of a convergent origin of tegminal stridulation and tibial tympana

From a morphological point of view, the hypothesis of a convergent origin of tegminal stridulation in Gryllidae, Gryllotalpidae, Tettigoniidae, and Prophalangopsidae is mainly based on differences found in the file-scraper mechanism and its behavioural context (Desutter-Grandcolas 2003). In males of these taxa, the tegminal stridulatory apparatus is composed of a raised toothed vein (the stridulatory file) situated on the underside of one tegmen contacting the scraper on the other tegmen during wing movement (Beier 1972). In Tettigoniidae the functional file is mainly placed on the left wing and the scraper on the right, thus bearing a left-over-right stridulation (Beier 1972). To the contrary, in most Gryllidae and Gryllotalpidae the position of stridulatory file and scraper is reversed and right-over-left stridulation is more common (Beier 1972). Whereas in the preceding taxa only a vestigial file is frequently present on the other wing (Chamorro-Rengifo *et al.* 2014), the tegmina of Prophalangopsidae have two functional stridulatory files and sounds are produced in either orientation (Morris & Gwynne 1978; Morris *et al.* 2002). In addition to the aforementioned differences, there is a longstanding discussion about the positional homology of the stridulatory vein (on which the file is located) among those singing taxa, that is either thought to be homologous (Zeuner 1939; Sharov 1968; Béthoux 2012) or not (e.g. Ander 1939; Ragge 1955; reviewed in Gwynne 1995). Also the convergent evolution of tympana represents a plausible evolutionary scenario. The origin of insect tympanal organs lies in a specialized anatomy and function of chordotonal organs (Fullard & Yack 1993). Chordotonal organs are located all over the insects' body and primarily function as mechanosensory organs in detecting movements of body components or vibrations (Yager 1999; Yack 2004). Insect ears have evolved 15 to 20 times independently in insects (Strauß & Stumpner 2015) and are regarded as structures that "are easy to make" (Fullard & Yack 1993). A tympanate insect ear is mainly composed of three different morphological and functional elements: the tympanum, a tracheal sac, and the tympanal organ itself (Yack 2004). In Ensifera, the tympanal organ is always

located in the proximal part of the tibia of both front legs thereof termed tibial organ (Yager 1999). The hypothesis of convergent origins of tympana among Ensifera gains support by anatomical differences mainly found between certain assisting components of their hearing organs. The tibial organ is accompanied by a tympanal trachea typically divided in two converging branches that are associated with the exteriorly visible tympana (Beier 1972; Michel 1974; Bailey 1993b). Based on their orientation, an anterior and a posterior tympanum on each tibia may be distinguished (Beier 1972). In Tettigoniidae, both tympana are about the same size and functional in sound detection (Yager 1999). In Gryllidae on the other hand the anterior tympanum is of exceedingly smaller size and plays only little, if any, role in sound reception (Ball & Young 1974; Michel 1974; Yager 1999). In the vast majority of Anostostomatidae two functional and equally sized tympana are found (Gibbs 1999; Brettschneider *et al.* 2007), whose structure and function is equivalent to those in Tettigoniidae (Nishino & Field 2003). Nevertheless, some anostostomatid genera only possess a single tympanum like *Transaevum* (Johns 1997) or *Gryllotaurus* (Karny 1937), but the anatomy of their tibial organs had never been investigated. Besides the morphology of their tympana, also further anatomical traits of the ensiferan ear provide good arguments for supporting the convergence hypothesis of tibial tympana. These differences refer to structures that improve the efficiency of processing auditory signals, viz. the acoustic trachea and the auditory spiracle. In contrast to members of the Caelifera, the mesothoracic stigma, or spiracle, of all ensiferans is covered by three lips (Desutter-Grandcolas 2003) and internally divided by a septum that separates two tracheal chambers: one for the leg trachea and one for the respiratory tracheae (Ander 1939; Beier 1972). Whereas the prothoracic stigma is closable in other tettigonioid lineages including *Cyphoderris* (Ball & Field 1981; Jeram *et al.* 1995; Strauß & Lakes-Harlan 2008a,b, 2010), the spiracle in tympanate Tettigoniidae forms two distinct openings, an auditory and a respiratory spiracle (Ander 1939; Beier 1972; Lakes-Harlan *et al.* 1991). This acoustic spiracle is regarded as the main sound input for the tibial organ (Strauß *et al.* 2014a), and the associated leg trachea is distinctly enlarged forming a *vesicula acustica*, or acoustic trachea, in Gryllidae (Schmidt & Römer 2013), Tettigoniidae (Ander 1939), and Prophalangopsidae (Ander 1939; Mason 1991). The leg tracheae of both body sides are connected by a transverse trachea that is likely present in all representatives of Ensifera (Ander 1939; Schmidt & Römer 2013). However,

Schmidt & Römer (2013) describe the transverse trachea to be absent in the cave-cricket *Troglophilus* thereby supposedly confirming a primary absence and thus plesiomorphic condition in Rhaphidophoridae. To the contrary, Ander (1939) found such a transverse trachea in the rhaphidophorid genera *Diestrammena* and *Rhaphidophora*, thus concluding that the absence of this trachea in *Troglophilus* represents a derived condition within Rhaphidophoridae. In tympanate Tettigoniidae, the transverse trachea is reduced to a fibrous filament impeding a communication between the *vesicula acustica* of both body sides (Ander 1939). In contrast, the transverse trachea of Gryllidae is typically enlarged and developed a medial septum enabling a directional hearing (Schmidt & Römer 2013).

The structure of the tibial organ in Ensifera

The sensory organ in the tibia of tettigonioids is composed of three functional components: subgenual organ, intermediate organ, and *crista acustica* (Strauß *et al.* 2014b). Interestingly, this threepartite composition of the tibial organ is found in all three leg pairs although a functional ear is only developed at the tibia of the front leg (Kalmring *et al.* 1994; Strauß & Lakes-Harlan 2008b, 2010). The most proximal part of the tibial organ, the subgenual organ, represents a highly sensitive vibration detector (Field & Matheson 1998; Yack 2004). The intermediate organ may be homologous to the distal organ found in Caelifera, Mantophasmatodea, Blattodea, and Phasmatodea and is likewise sensitive to vibrational signals (Eberhard *et al.* 2010; Strauß & Lakes-Harlan 2013; Strauß *et al.* 2014b). In combination with a tympanum and an enlarged acoustic trachea developed in the forelegs, the distal most part of the hearing organ of bush-crickets, the *crista acustica*, functions as a true auditory receptor that is sensitive to airborne sounds (Rössler *et al.* 2006). The auditory sensilla in the *crista acustica* are linearly arranged and respond to specific sound frequencies, resembling the structure of the auditory sensilla in the cochlea of the mammalian ear (Hoy 2012; Montealegre-Z *et al.* 2012). A morphologically similar organ to the *crista acustica* likewise composed of linearly arranged sensilla is present in Grylloidea which is termed the tympanal organ, but its homology is, however, not sufficiently resolved (Beier 1972; Strauß *et al.* 2014b). Nevertheless, a homologue to the *crista acustica* of Tettigoniidae is present in atympanate tettigonioid taxa like *Stenopelmatus* (Stenopelmatidae) (Strauß & Lakes-Harlan 2008b), *Comicus* (Schizodactylidae) (Strauß & Lakes-Harlan 2009, 2010), and *Ametrus* (Gryllacrididae)

(Strauß & Lakes-Harlan 2008a). In those deaf taxa, the *crista acustica* homologue is thought to further improve the sensitivity or detection of different vibration waves and related parameters, like displacement or velocity (Strauß & Lakes-Harlan 2008b).

To the contrary, the hearing organ of cave crickets (Rhaphidophoridae) entirely lacks such a homologue to the *crista acustica* (Jeram *et al.* 1995; Strauß *et al.* 2014b). Based on previously presented ensiferan phylogenies, in which Rhaphidophoridae form a basal lineage of the tettigonioid clade forming the sister to all the remaining tettigonioid taxa (Gwynne 1995; Desutter-Grandcolas 2003), the lack of the *crista acustica* in cave crickets was thought to represent the plesiomorphic condition of Ensifera (Strauß *et al.* 2014b). This assumption favoured the scenario of a non-stridulating and non-hearing ensiferan ancestor supposing a step-wise evolution of the hearing organs and related stridulatory mechanisms (Desutter-Grandcolas 2003). An updated, comprehensive molecular phylogeny of Ensifera placed the Rhaphidophoridae not as a basal tettigonioid clade, but as a more subordinate group, namely as sister to Prophalangopsidae and Stenopelmatoidea (including Stenopelmatidae, Anostostomatidae, and Gryllacrididae) (Song *et al.* 2015). This phylogenetic hypothesis, as well as that presented in this study, rejects the thesis of a primarily simple structure of the hearing organ in cave crickets. Nonetheless, Strauß *et al.* (2014b) did not preclude the possibility of a secondarily simplified structure of the tibial organ of cave crickets, although its anatomy largely resembles that of grasshoppers and stick and leaf insects. With an estimated age of at least 140 million years (Allegrucci *et al.* 2010; Song *et al.* 2015), Rhaphidophoridae forms one of the oldest exclusively wingless ensiferan lineages. In addition, neither an inter- nor an intraspecific stridulatory and acoustic mechanism of communication is known from Rhaphidophoridae (Weissmann 1997). Therefore, a possible explanation for the simplified tibial organ in cave crickets might be a rather complete reduction of hearing in the course of evolution due to the lack of usage as specialized cave dwellers (Mahner & Bunge 1997).

The relation between communicational mode and the presence of tympana

The intraspecific communication mechanism in cave crickets (Rhaphidophoridae) (Weissmann 2001), raspy crickets (Gryllacrididae) (Rentz 1996; Hale & Rentz 2001), and Jerusalem crickets (Stenopelmatidae) (Weissmann 2001) is based on signals that are

transmitted by substrate drumming. The communication by vibratory signals is present in nearly all major insect lineages, and is thereof frequently regarded as the ancestral form of communication in insects (Virant-Doberlet & Cockl 2004; Cocroft & Rodríguez 2005; Eberhard *et al.* 2010). As stated above, there is virtually no doubt that the tibial organ in the last common ancestor of bush-crickets (Tettigoniidae) was equipped with a tympanum and fully functional as an auditory organ (Beier 1972). Beside bush-crickets (Tettigoniidae) and hump-winged crickets (Prophalangopsidae), tympana in the foreleg are only known from a single further taxon of the tettigonioid clade, from Anostostomatidae (king crickets and wetas (Gorochov 2001). However, a tympanum is frequently absent in American (Caudell 1916; Gorochov 2001) and African anostostomatid genera (Brettschneider *et al.* 2007). A femoro-abdominal stridulatory apparatus is described for a number of genera, e.g. *Hemiandrus* (Taylor-Smith *et al.* 2016), *Hemideina* (Field 1993a), *Motuweta* (Johns 1997), *Anisoura* (Ander 1933), and *Libanasa* (Johns & Hemp 2015). Unfortunately, many taxonomic descriptions of further anostostomatid genera lack information about the presence or absence of a femoro-abdominal stridulatory organ (Willemse 1963; Brettschneider *et al.* 2007; Derka & Fedor 2010; Heleodoro & de Mello Mendes 2016). Behavioural studies of the usage of this femoro-abdominal stridulatory apparatus in anostostomatids are sparse. Only anostostomatids from Australia and New Zealand (only those are called wetas) (Field 1993b, 2001; McVean & Field 1996; Field & Glasgow 2001) and the African genus *Libanasidus* (Bateman & Toms 1998) are sufficiently studied concerning their acoustic behaviour. In these taxa, the femoro-abdominal stridulatory mechanism is used in two differing contexts: for defence against predators or to communicate with conspecifics (Field 1993b; McVean & Field 1996). Interestingly, both strategies are accompanied by different behaviours. When defending themselves from predators, tree wetas hold their hind leg straightened above the body producing the sound by a downward rotation of the hind leg (McVean & Field 1996). In contrast, all six legs stay on the substrate when tree wetas communicate in a social context, the signal is produced by a rapid oscillation of the abdomen against the femoral pegs and contains vibratory and auditory elements (McVean & Field 1996). Like in the prophalangopsid *Cyphoderris*, this intraspecific stridulatory mechanism is rather used in male-male-interactions than for attracting females (Field 1993a; Bateman & Toms 1998). Femoro-abdominal stridulation in an inter-male context is solely described for New Zealand tree and giant wetas, the genera *Hemideina* and *Deinacrida* (Field 1993b, 2001),

and in the African king cricket *Libanasidus* (Bateman & Toms 1998). In those genera that are shown to communicate by airborne sounds in an intraspecific context, tympana are always present (Field 2001; Brettschneider *et al.* 2007). The only weta genus in which a tympanum is absent, is the ground weta (*Hemiandrus*) (Field 2001; Taylor-Smith *et al.* 2016). *Hemiandrus* also has a femoro-abdominal stridulatory organ, but it is solely used in an interspecific context (Field & Glasgow 2001). In contrast to tree and giant wetas, conspecifics of ground wetas communicate by drumming their abdomen onto the substrate (Field & Glasgow 2001), resembling the intraspecific communicational mode of Stenopelmatidae, Gryllacrididae, and Rhaphidophoridae. Therefore, as in the singing taxa Tettigoniidae, Gryllidae, Gryllotalpidae, and Prophalangopsidae, a tympanum might only be present in those anostostomatid taxa that show a stridulatory behaviour that is used in an intraspecific context, even in taxa with a further alternative stridulatory mechanism: in the tympanate anostostomatid genera *Anisoura* and *Motuweta* (Field & Deans 2001), large mandibular tusks bear stridulatory tubercles or ridges that produce a sound when the mandibles are opened and are used in male agonistic interactions (Field & Deans 2001).

Rather than assuming the losses of acoustical hearing, the tympanum and assisting auditory structures in the sister taxon of Tettigoniidae it is most likely that the last common ancestor of the whole tettigonioid clade neither had auditory structures nor the ability to hear acoustic signals. Nevertheless, the tettigonioid ancestor likely had a tripartite tibial organ with a *crista acustica* homologue in all three leg pairs. The *crista acustica* homologue might have improved the sensitivity or detection of vibrational signals and enhanced the primarily intraspecific communication by substrate drumming. Consequently, this specific structure of the tibial organ might have served as a prerequisite for the independent evolution of a functional ear at the tibia of the forelegs within the tettigonioid clade. This functional tettigonioid ear was composed of tympana and assisting auditory structures like the *vesicula acustica* in only those taxa developing an acoustic intraspecific communicational mechanism. A likewise increased vibrational sensitivity of a chordotonal organ in atympanate flies was previously shown to evolve into nearly identical and thus apparently homologous hearing organs in two distant lineages of parasitoid flies (Lakes-Harlan *et al.* 1999). The evolution of tettigonioid ears thereby adds

another example highlighting the *crista acustica* homologue with its increased sensitivity as a key innovation for the evolutionary pathway developing insect ears.

Conclusions and outlook

The present study is a significant step towards a deeper understanding of the evolution of thoracic characters within Polyneoptera, and in Orthoptera in particular. In addition, it is demonstrated that this character system is of considerable value for the reconstruction of phylogenetic relationships in Polyneoptera and Orthoptera. However, even more reliable results in reconstructing phylogenetic relationships based on morphological data can be expected when further character complexes are included in the analysis. The next step there-fore requires to combine the characters of the thoracic skeleton of the investigated Polyneoptera with further available data on, e.g. the morphology of the head (Wipfler *et al.* 2011; Friedemann *et al.* 2012) and tarsal attachment structures (Beutel & Gorb 2006, 2008). In addition, much more research is needed on character systems currently not sufficiently studied in a comprehensive approach, like e.g. the preabdomen (Klug & Bradler 2006) or genitalia (Klass & Ulbricht 2009; Chamorro-Rengifo & Lopes-Andrade 2014; Gorochov 2014). Although the potential for reconstructing phylogenetic relationships based on morphological characters is limited, nowadays largely replaced by molecular phylogenies, morphology still plays an essential role in visualizing the evolutionary history on the phenotypic level by adding further explanations on form and function of certain morphological structures, as well as their evolutionary changes and modifications (Friedrich *et al.* 2013; Giribet 2015).

References

Albrecht, F. O. 1953. *The Anatomy of the Migratory Locust*. University of London, Athlone Press, Western Printing Services Ltd., London, 1-118 pp.

Alexander, R. D. 1962. Evolutionary change in cricket acoustical communication. *Evolution*, **16**, 443–467.

Alicata, P. 1962. Morfologia comparata ed evoluzione della regione del collo negli Ortotteri. *Bolletino di Zoologia*, **29**, 49–72.

Allegrucci, G., Trewick, S. A., Fortunato, A., Carchini, G. & Sbordoni, V. 2010. Cave crickets and cave weta (Orthoptera, Rhaphidophoridae) from the southern end of the World : a molecular phylogeny test of biogeographical hypotheses. *Journal of Orthoptera Research*, **19**, 121–130.

Ander, K. 1933. Über *Anisoura nicobarica* m., eine bemerkenswerte Laubheuschrecke aus der Familie Gryllacrididae (Orth. Saltatoria). *Konowia*, **12**, 217–230.

Ander, K. 1938. Ein abdominales Stridulationsorgan bei *Cyphoderris* (Prophalangopsidae) und über die systematische Einteilung der Ensiferen (Saltatoria). *Opuscula Entomologica*, **3**, 32–38.

Ander, K. 1939. Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria). *Opuscula Entomologica Supplementum II*, 1–306.

Badonell, A. 1934. Recherches sur l'anatomie des Psoque. *Bulletin Biologique de la France et de la Belgique*, **18**, 1–241.

Bailey, W. J. 1993. The tettigoniid (Orthoptera: Tettigoniidae) ear: multiple functions and structural diversity. *International Journal of Insect Morphology and Embryology*, **22**, 185–205.

Bailey, W. J. & Kamien, D. 2001. Hearing dimorphism, trait variation and conflicts over space in the thorax of the bushcricket *Requena verticalis* (Listroscelidinae: Tettigoniidae: Orthoptera). *Journal of Comparative Physiology A*, **187**, 647–652.

Bailey, W. J. & Römer, H. 1991. Sexual differences in auditory sensitivity: mismatch of hearing threshold and call frequency in a tettigoniid (Orthoptera, Tettigoniidae: Zaprochilinae). *Journal of Comparative Physiology A*, **169**, 349–353.

Ball, E. & Field, L. H. 1981. Cell and tissue structure of the auditory system of the weta *Hemideina crassidens* (Blanchard , 1851). *Cell and Tissue Research*, **217**, 321–343.

Ball, E. & Young, D. 1974. Structure and development of the auditory system in the prothoracic leg of the cricket *Teleogryllus commodus* (Walker). *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **147**, 313–324.

Barlet, J. 1985a. La musculature pterothoracique d'une *Embia* femelle (Insectes, Embiopteres). *Bulletin de la Société Royale des Sciences de Liège*, **54**, 140–148.

Barlet, J. 1985b. La musculature thoracique d'*Hemimerus bouvieri* CHPD (Dermaptères). *Bulletin et Annales de la Société Royale Belge d'Entomologie*, **121**, 169–195.

Barlet, J. 1985c. Le pterothorax du male d'*Embia surcoufi* Navas (Insectes, Embiopteres). *Bulletin de la Société Royale des Sciences de Liège*, **54**, 349–362.

Barlet, J. 1985d. Le squelette pterothoracique d'une femelle d'*Embia* (Insectes, Embiopteres). *Bulletin de la Société Royale des Sciences de Liège*, **54**, 133–139.

Bateman, P. & Toms, R. 1998. Mating, mate guarding and male-male relative strength assessment in an African king cricket (Orthoptera: Mimnermidae). *Transactions of the American Entomological Society*, **124**, 69–75.

Beier, M. 1968a. Mantodea (Fangheuschrecken). *In*: Helmcke, J., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–47.

Beier, M. 1968b. Phasmida (Stab- oder Gespenstschrecken). *In*: Helmcke, J., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–56.

Beier, M. 1972. Saltatoria (Grillen und Heuschrecken). *In*: Helmcke, J. G., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–217.

Beier, M. 1974. Blattariae (Schaben). *In*: Helmcke, J., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–127.

Belwood, J. 1990. Anti-predator defences and ecology of neotropical forest katydids, especially the Pseudophyllinae. *In*: Bailey, W. J. & Rentz, D. C. F. (eds) *The Tettigoniidae. Biology, Systematics and Evolution.* Springer-Verlag Berlin Heidelberg GmbH, Berlin, Heidelberg, New York, 8–26.

Béthoux, O. 2005. Wing venation pattern of Plecoptera (Insecta: Neoptera). *Illiesia*, **1**, 52–81.

Béthoux, O. 2007. Cladotypic taxonomy applied: Titanopterans are Orthopterans. *Arthropod Systematics & Phylogeny*, **65**, 135–156.

Béthoux, O. 2012. *Grylloptera* - A unique origin of the stridulatory file in katydids, crickets, and their kin (Archaeorthoptera). *Arthropod Systematics & Phylogeny*, **70**, 43–68.

Béthoux, O. & Nel, A. 2001. Venation pattern of Orthoptera. *Journal of Orthoptera Research*, **10**, 195–198.

Beutel, R. G. & Gorb, S. N. 2001. Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. *Journal of Zoological Systematics and Evolutionary Research*, **39**, 177–207.

Beutel, R. G. & Gorb, S. N. 2006. A revised interpretation of the evolution of attachment structures in Hexapoda with special emphasis on Mantophasmatodea. *Arthropod Systematics & Phylogeny*, **64**, 3–25.

Beutel, R. G. & Gorb, S. N. 2008. Evolutionary scenarios for unusual attachment devices of Phasmatodea and Mantophasmatodea (Insecta). *Systematic Entomology*, **33**, 501–510.

Beutel, R. G. & Leschen, R. A. B. 2005. Coleoptera, Beetles. Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polphaga partim). *In*: Kristensen, N. P. & Beutel, R. G. (eds) *Handbook of Zoology*. Walter De Gruyter & Co, Berlin, 1–567.

Beutel, R. G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., Meier, R., Misof, B., Whiting, M. F. & Vilhelmsen, L. 2011. Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. *Cladistics*, **27**, 341–355.

Beutel, R. G., Wipfler, B., Gottardo, M. & Dallai, R. 2013. Polyneoptera or 'Lower Neoptera' - new light on old and difficult phylogenetic problems. *Atti Accademia Nazionale Italiana di Entomologica*, **61**, 133–142.

Bharadwaj, R. K. & Chadwick, L. E. 1974a. Postembryonic development of the cervico-thoracic muscles of *Euborellia annulipes* (Lucas) (Dermaptera: Labiduridae). *Journal of Morphology*, **143**, 457–473.

Bharadwaj, R. K. & Chadwick, L. E. 1974b. Postembryonic development of the cervico-thoracic skeleton of *Euborellia annulipes* (Lucas) (Dermaptera: Labiduridae). *Journal of Morphology*, **143**, 457–473.

Blackith, R. E. & Blackith, R. M. 1966. The anatomy and physiology of the morabine grasshoppers II. External anatomy and comparisons with Pyrgomorphidae, Acrididae, and Proscopiidae. *Australian Journal of Zoology*, **14**, 1035–1071.

Blackith, R. E. & Blackith, R. M. 1967. The anatomy and physiology of the morabine grasshoppers. III. Muscles, nerves, tracheae, and genitalia. *Australian Journal of Zoology*, **15**, 961–998.

Blackith, R. E. & Blackith, R. M. 1969. Variation of shape and of discrete anatomical characters in the morabine grasshoppers. *Australian Journal of Zoology*, **17**, 697–718.

Bradler, S. 2009. Phylogeny of the stick and leaf insects (Insecta: Phasmatodea). *Species, Phylogeny and Evolution*, **2**, 3–139.

Bremer, K. 1994. Branch support and tree stability. *Cladistics*, **10**, 295–304.

Brettschneider, H., Chimimba, C. T., Scholtz, C. H. & Bateman, P. W. 2007. Review of southern African Anostostomatidae (Orthoptera : Ensifera), with a key to genera. *African Entomology*, **15**, 103–119.

Carbonell, C. S. 1947. The thoracic muscles of the cockroach *Periplaneta americana* (L.). *Smithsonian Miscellaneous Collections*, **107**, 1–23.

Carpentier, F. 1921a. Pterothorax et prothorax. Étude des segments thoraciques d'un orthoptère. *Annales de la Société Entomologique de Belgique*, **61**, 337–343.

Carpentier, F. 1921b. Sur l'endosquelette prothoracique de *Gryllotalpa vulgaris*. *Bulletin de la Classe des Sciences, Académie Royale de Belgique*, **7**, 125–134.

Carpentier, F. 1923. Musculature et squelette chitineux: Recherches sur le comportement de la musculature des flancs dans les segments cryptopleuriens du thorax chez les orthoptères. *Mémoires de l'Académie Royale de Belgique (2). Collection in -8°*, **7 (3)**, 1–56.

Carpentier, F. 1936. Le thorax et ses appendices chez les vrais et les faux Gryllotalpides. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique. 2ème Série*, **4**, 3–86.

Caudell, A. N. 1916. The genera of the tettiginiid insects of the family Rhaphidophorinae found in America north of Mexico. *Proceedings of the United States National Museum*, **49**, 655–690.

Chamorro-Rengifo, J. & Lopes-Andrade, C. 2014. The phallus in Tettigoniidae (Insecta: Orthoptera: Ensifera): revision of morphology and terminology, and discussion on its taxonomic importance and evolution. *Zootaxa*, **3815**, 151–199.

Chamorro-Rengifo, J., Braun, H. & Lopes-Andrade, C. 2014. The secret stridulatory file under the right tegmen in katydids (Orthoptera, Ensifera, Tettigonioidea). *Zootaxa*, **3821**, 590–596.

Chintauan-Marquier, I. C., Legendre, F., Hugel, S., Robillard, T., Grandcolas, P., Nel, A., Zuccon, D. & Desutter-Grandcolas, L. 2016. Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. *Cladistics*, **32**, 54–81.

Cocroft, R. B. & Rodríguez, R. L. 2005. The behavioral ecology of insect vibrational communication. *BioScience*, **55**, 323–334.

Crampton, G. C. 1926. A comparison of the neck and prothoracic sclerites trought the orders of insects from the standpoint of phylogeny. *Transactions of the American Entomological Society*, **52**, 199–248.

Czihak, G. 1954. Beiträge zur Anatomie des Thorax von *Ascalaphus macaronius* Scop., *Myrmeleon europaeus* McLach und *Palpares libelluloides* Dalm. *Österreichische Zoologische Zeitschrift*, **4**, 421–448.

Dambach, M. & Lichtenstein, L. 1978. Zur Ethologie der afrikanischen Grille *Phaeophilacris spectrum* Saussure. *Zeitschrift für Tierphysiologie*, **46**, 14–29.

de Mello, F. de A. G. & dos Reis, J. C. 1994. Substrate drumming and wing stridulation performed during courtship by a new Brazilian cricket (Orthoptera: Grylloidea: Phalangopsidae). *Journal of Orthoptera Research*, **2**, 21–24.

de Zolessi, L. C. 1968. Morphologie, endosquelette et musculature d'un acridien aptère (Orthoptera: Proscopiidae). *Transactions of the Royal Entomological Society of London*, **120**, 55–113.

Derka, T. & Fedor, P. 2010. *Hydrolutos breweri* sp. n., a new aquatic Lutosini species (Orthoptera: Anostostomatidae) from Churí-tepui (Chimantá Massif, Venezuela). *Zootaxa*, **2653**, 51–59.

Desutter-Grandcolas, L. 1997. A phylogenetic analysis of the evolution of the stridulatory apparatus in true crickets (Orthoptera, Grylloidea). *Cladistics*, **13**, 101–108.

Desutter-Grandcolas, L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta*, **32**, 525–561.

Eades, D. C., Otte, D., Cigliano, M. M. & Braun, H. 2015. Orthoptera Species File. Version 5.0/5.0. http://orthoptera.speciesfile.org. Accessed 13 Feb 2017.

Eberhard, M. J. B., Lang, D., Metscher, B., Pass, G., Picker, M. D. & Wolf, H. 2010. Structure and sensory physiology of the leg scolopidial organs in Mantophasmatodea and their role in vibrational communication. *Arthropod Structure & Development*, **39**, 230–241.

Engel, M. & Grimaldi, D. 2000. A winged *Zorotypus* in Miocene Amber from the Dominician Republic (Zoraptera: Zorotypidae), with discussion on relationships of and within the order. *Acta Geológica Hispánica*, **35**, 149–164.

Engel, M. S., Davis, S. R. & Prokop, J. 2013. Insect wings: the evolutionary development of nature's first flyers. *In*: Minelli, A., Boxshall, G. & Fusco, G. (eds) *Arthropod Biology and Evolution*. Springer-Verlag, Berlin, Heidelberg, 269–298.

Ewer, D. W. 1954. A Note on the comparative anatomy of the pterothorax of macropterous and brachypterous forms of the grasshopper *Zonocerus elegans* Thunb. *Journal of the Entomological Society of Southern Africa*, **17**, 237–240.

Ewer, D. W. 1958. Notes on acridid anatomy. V. The pterothoracic musculature of *Lentula callani* Dirsh. *Journal of the Entomological Society of Southern Africa*, **21**, 132–138.

Field, L. H. 1993a. Observations on stridulatory, agonistic, and mating behaviour of Hemideina ricta (Stenopelmatidae : Orthoptera), the rare Banks Peninsula weta. *New Zealand Entomologist*, **16**, 68–74.

Field, L. H. 1993b. Structure and evolution of stridulatory mechanisms in New Zealand wetas (Orthoptera: Stenopelmatidae). *International Journal of Insect Morphology and Embryology*, **22**, 163–183.

Field, L. H. 2001. Stridulatory mechanisms and associated behaviour in New Zealand Wetas. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 271–295.

Field, L. H. & Bailey, W. J. 1997. Sound production in primitive Orthoptera from Western Australia: sounds used in defence and social communication in *Ametrus* sp. and *Hadrogryllacris* sp. (Gryllacrididae: Orthoptera). *Journal of Natural History*, **31**, 1127–1141.

Field, L. H. & Deans, N. A. 2001. Sexual selection and secondary sexual characters of wetas and king crickets. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 179–204.

Field, L. H. & Glasgow, S. 2001. Defence behaviour. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 297–316.

Field, L. H. & Matheson, T. 1998. Chordotonal organs of insects. *Advances in Insect Physiology*, **27**, 1–230.

Flook, P. K., Klee, S. & Rowell, C. H. 1999. Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. *Systematic Biology*, **48**, 233–253.

Friedemann, K., Wipfler, B., Bradler, S. & Beutel, R. G. 2012. On the head morphology of *Phyllium* and the phylogenetic relationships of Phasmatodea (Insecta). *Acta Zoologica*, **93**, 184–199.

Friedrich, F. & Beutel, R. G. 2008. The thorax of *Zorotypus* (Hexapoda, Zoraptera) and a new nomenclature for the musculature of Neoptera. *Arthropod Structure & Development*, **37**, 29–54.

Friedrich, F. & Beutel, R. G. 2010. Goodbye Halteria? The thoracic morphology of Endopterygota (Insecta) and its phylogenetic implications. *Cladistics*, **26**, 579–612.

Friedrich, F., Farrell, B. D. & Beutel, R. G. 2009. The thoracic morphology of Archostemata and the relationships of the extant suborders of Coleoptera (Hexapoda). *Cladistics*, **25**, 1–37.

Friedrich, F., Matsumura, Y., Pohl, H., Bai, M., Hörnschemeyer, T. & Beutel, R. G. 2013. Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. *Entomological Science*, **17**, 1–24.

Fullard, J. H. & Yack, J. E. 1993. The evolutionary biology of insect hearing. *Trends in Ecology & Evolution*, **8**, 248–252.

Gibbs, G. W. 1999. Four new species of giant weta, *Deinacrida* (Orthoptera: Anostostomatidae: Deinacridinae) from New Zealand . *Journal of the Royal Society of New Zealand*, **29**, 307–324.

Giribet, G. 2015. Morphology should not be forgotten in the era of genomics—a phylogenetic perspective. *Zoologischer Anzeiger - A Journal of Comparative Zoology*, **256**, 96–103.

Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.

Gorochov, A. V. 2014. Evolution and taxonomic significance of the copulatory apparatus in Ensifera (Orthoptera). Part 1: General concepts and origin. *Zoosystematica Rossica*, **23**, 197–209.

Gorochov, A. V. 1995a. Contribution to the system and evolution of the order Orthoptera. *Zoologichesky Zhurnal*, **74**, 39–45.

Gorochov, A. V. 1995b. System and evolution of the suborder Ensifera (Orthoptera). *Proceedings of the Zoological Institute, Russian Academy of Sciences*, 1–224 (in Russian).

Gorochov, A. V. 2001. The higher classification, phylogeny and evolution of the superfamily Stenopelmatoidea. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 3–34.

Greenfield, M. D. 1997. Acoustic communication in Orthoptera. *In*: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds) *The Bionomics of Grasshoppers, Katydids and Their Kin*. CAB International, Wallingford, New York, 197–230.

Grimaldi, D. & Engel, M. S. 2005. *Evolution of the Insects*. Cambridge University Press, New York, 772pp.

Günther, K. & Herter, K. 1974. Dermaptera (Ohrwürmer). *In*: Helmcke, J., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–158.

Gurney, A. B. 1935. The external morphology and phylogenetic position of the Woodland Cave Cricket *(Ceuthophilus brevipes* Scudder; Orthoptera; Tettigoniidæ). University of Massachusetts Amherst, 1-46 pp.

Gwynne, D. T. 1995. Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research*, **4**, 203–218.

Gwynne, D. T. 2001. Entomological choristers: song and mate attraction. *In*: Alcock, J. (ed.) *Katydids and Bush-Crickets: Reproductive Behaviour and Evolution of the Tettigoniidae*. Cornell University Press, Ithaca, London, 89–121.

Gwynne, D. T. 2004. Reproductive behavior of ground weta (Orthoptera: Anostostomatidae): drumming behavior, nuptial feeding, post-copulatory guarding and maternal ccare. *Journal of the Kansas Entomological Society*, **77**, 414–428.

Hale, R. J. & Rentz, D. C. F. 2001. The Gryllacrididae: an overview of the world fauna with emphasis on Australian examples. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 95–110.

Heleodoro, R. A. & de Mello Mendes, D. M. 2016. Description of a new species of *Lutosa* Walker, 1869 (Orthoptera: Anostostomatidae: Lutosinae) from the Brazilian Atlantic Forest, with biological and behavioral information. *Zootaxa*, **4189**, 387–394.

Heller, K.-G. 1986. Warm-Up and stridulation in the bushcricket, *Hexacentrus unicolor* Serville (Orthoptera, Conocephalidae, Listroscelidinae). *The Journal of Experimental Biology*, **109**, 97–109.

Heller, K.-G. 1996. Unusual abdomino-alary, defensive stridulatory mechanism in the bushcricket *Pantecphylus cerambycinus* (Orthoptera, Tettigonioidea, Pseudophyllidae). *Journal of Morphology*, **227**, 81–86.

Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin, 370 pp.

Hill, P. S. M. 1999. Lekking in *Gryllotalpa major*, the prairie mole cricket (Insecta: Gryllotalpidae). *Ethology*, **105**, 531–545.

Hill, P. S. M., Hoffart, C. & Buchheim, M. 2002. Tracing phylogenetic relationships in the family Gryllotalpidae. *Journal of Orthoptera Research*, **11**, 169–174.

Hörnschemeyer, T. 2002. Phylogenetic significance of the wing-base of the Holometabola (Insecta). *Zoologica Scripta*, **31**, 17–29.

Howard, D. R. & Hill, P. S. M. 2006. Morphology and calling song characteristics in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *Journal of Orthoptera Research*, **15**, 53–57.

Howard, D. R., Mason, A. C. & Hill, P. S. M. 2008. Hearing and spatial behavior in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *Journal of Experimental Biology*, **211**, 3613–3618.

Hoy, R. R. 2012. Convergent evolution of hearing. *Science*, **338**, 894–895.

Hubbell, T. H. & Norton, R. M. 1978. The systematics and biology of the cave-crickets of the North American tribe Hadenoecini (Orthoptera Saltatoria: Esifera: Rhaphidophoridae: Dolichopodinae). *Miscellaneous Publications Museum of Zoology, University of Michigan*, **156**, 1–124.

Irish, J. 1986. The species of *Comicus* Brunner v. Wattenwyl (Orthoptera: Schizodactylidae) with a discussion of their origin. *Navorsinge van die Nasionale Museum Bloemfontein*, **5**, 253–276.

Ishiwata, K., Sasaki, G., Ogawa, J., Miyata, T. & Su, Z. H. 2011. Phylogenetic relationships among insect orders based on three nuclear protein-coding gene sequences. *Molecular Phylogenetics and Evolution*, **58**, 169–180.

Jeram, S., Rössler, W., Cokl, A. & Kalmring, K. 1995. Structure of atympanate tibial organs in legs of the cave-living Ensifera, *Troglophilus neglectus* (Gryllacridoidea, Raphidophoridae). *Journal of Morphology*, **223**, 109–118.

Jeziorski, L. 1918. Der Thorax von *Dixippus morosus* (*Carausius*). *Zeitschrift für Wissenschaftliche Zoologie*, **117**, 727–815.

Johns, P. M. & Hemp, C. 2015. Redescription of *Libanasa brachyura* Karny, 1928. (Orthoptera: Anostostomatidae: ?Lutosinae) from Tanzania and problems at the subfamily level. *Zootaxa*, **3946**, 113–124.

Johns, P. M. M. 1997. The Gondwanaland Weta: family Anostostomatidae (formerly in Stenopelmatidae, Henicidae or Mimnermidae): nomenclatural problems, world checklist, new genera and species. *Journal of Orthoptera Research*, **6**, 125–138.

Jost, M. C. & Shaw, K. L. 2006. Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution*, **38**, 510–530.

Kalmring, K., Rössler, W. & Unrast, C. 1994. Complex tibial organs in the forelegs, midlegs, and hindlegs of the bushcricket *Gampsocleis gratiosa* (Tettigoniidae): comparison of the physiology of the organs. *Journal of Experimental Zoology*, **270**, 155–161.

Karny, H. H. 1937. Orthoptera. Fam. Gryllacrididae. *Genera Insectorum*, **206**, 1–317.

Kevan, D. K. M. 1982. Orthoptera. *In*: Parker, S. P. (ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill, Inc., New York, 352–379.

Khattar, N. 1960. On the morphology of the neck and thorax of *Schizodactylus monstrosus* Don. *Journal of the Zoological Society of India*, **12**, 162–174.

Khattar, N. 1972. A description of the adult and the nymphal stages of *Schizodactylus monstrosus* (Drury) (Orthoptera). *Journal of Natural History*, **6**, 589–600.

Khattar, N. & Srivastava, R. P. 1962. Morphology of the pterothorax of *Schizodactylus monstrosus* Don. (Orthoptera). *Journal of the Zoological Society of India*, **14**, 93–108.

Kjer, K. M., Carle, F. L., Litman, J. & Ware, J. 2006. A molecular phylogeny of Hexapoda. *Arthropod Systematics & Phylogeny*, **64**, 35–44.

Klass, K.-D. 2007. Die Stammesgeschichte der Hexapoden: eine kritische Diskussion neuerer Daten und Hypothesen. *Denisia*, **20**, 413–450.

Klass, K.-D., Zompro, O., Kristensen, N. P. & Adis, J. 2002. Mantophasmatodea: a new insect order with extant members in the Afrotropics. *Science*, **296**, 1456–1459.

Klass, K. D. & Ulbricht, J. 2009. The female genitalic region and gonoducts of Embioptera (Insecta), with general discussions on female genitalia in insects. *Organisms Diversity and Evolution*, **9**, 115–154.

Kleinow, W. 1966. Untersuchungen zum Flügelmechanismus der Dermapteren. *Zoomorphology*, **56**, 363–416.

Klug, R. 2008. *Anatomie des Pterothorax der Phasmatodea, Mantophasmatodea und Embioptera und seine Bedeutung für die Phylogenie der Polyneoptera (Insecta).* Georg-August-Universität Göttingen, 1-126 pp.

Klug, R. & Bradler, S. 2006. The pregenital abdominal musculature in phasmids and its implications for the basal phylogeny of Phasmatodea (Insecta: Polyneoptera). *Organisms Diversity and Evolution*, **6**, 171–184.

Kluge, N. J. 2016. Structure of ovipositors and cladoendesis of Saltatoria, or Orchesopia. *Entomological Review*, **96**, 1015–1040.

Koeth, M., Friedrich, F., Pohl, H. & Beutel, R. G. 2012. The thoracic skeleto-muscular system of *Mengenilla* (Strepsiptera: Mengenillidae) and its phylogenetic implications. *Arthropod Structure & Development*, **41**, 323–335.

Korsunovskaya, O. S. 2008. Acoustic signals in katydids (Orthoptera, Tettigonidae). Communication 1. *Entomological Review*, **88**, 1032–1050.

Kramer, S. 1944. The external morphology of the oblong-winged katydid, *Amblycorypha oblongifolia* (DeGEER) (Orthoptera, Tettigoniidae). *Annals of the Entomological Society of America*, **37**, 167–192.

Kristensen, N. P. 1975. The phylogeny of hexapod 'orders'. A critical review of recent accounts. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **13**, 1–44.

Kristensen, N. P. 1981. Phylogeny of insect orders. *Annual Review of Entomology*, **26**, 135–157.

Kristensen, N. P. 1991. Phylogeny of extant hexapods. *In*: *The Insects of Australia: A Textbook for Students and Research Workers*. 125–140.

La Greca, M. 1938. La muscolatura di *Gryllotalpa gryllotalpa* (L.). *Archivio Zoologico Italiano*, **27**, 217–319.

Lakes-Harlan, R., Bailey, W. J. & Schikorski, T. 1991. The auditory system of an atympanate bushcricket *Phasmodes ranatriformes* (Westwood) (Tettigoniidae: Orthoptera). *The Journal of Experimental Biology*, **158**, 307–324.

Lakes-Harlan, R., Stölting, H. & Stumpner, A. 1999. Convergent evolution of insect hearing organs from a preadaptive structure. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1161.

Legendre, F., Robillard, T., Song, H., Whiting, M. F. & Desutter-Grandcolas, L. 2010. One hundred years of instability in ensiferan relationships. *Systematic Entomology*, **35**, 475–488.

Lehmann, G. U. C., Strauß, J. & Lakes-Harlan, R. 2007. Listening when there is no sexual signalling? Maintenance of hearing in the asexual bushcricket *Poecilimon intermedius*. *Journal of Comparative Physiology A*, **193**, 537–545.

Letsch, H. & Simon, S. 2013. Insect phylogenomics: new insights on the relationships of lower neopteran orders (Polyneoptera). *Systematic Entomology*, **38**, 783–793.

Leubner, F., Hörnschemeyer, T. & Bradler, S. 2016. The thorax of the cave cricket *Troglophilus neglectus*: anatomical adaptations in an ancient wingless insect lineage (Orthoptera: Rhaphidophoridae). *BMC Evolutionary Biology*, **16**, 39.

Leubner, F., Bradler, S. & Wipfler, B. 2017. The thoracic morphology of the wingless dune cricket *Comicus calcaris* (Orthoptera: Schizodactylidae): novel apomorphic characters for the group and adaptations to sand desert environments. *Arthropod Structure & Development*, 46, 449–461.

Levereault, P. 1938. The morphology of the Carolina mantis. *The University of Kansas Science Bulletin*, **25**, 577–633.

Lloyd, J. E. & Gurney, A. B. 1975. Labral stridulation in a katydid (a coconut-infesting 'treehopper') (Orthoptera: Tettigoniidae: Mecopodinae). *Entomological News*, **86**, 47–50.

Lunichkin, A. M., Zhemchuzhnikov, M. K. & Knyazev, A. N. 2016. Basic elements of behavior of the cricket *Phaeophilacris bredoides* Kaltenbach (Orthoptera, Gryllidae). *Entomological Review*, **96**, 537–544.

Mahner, M. & Bunge, M. 1997. *Foundations on Biophilosophy*. Springer-Verlag, Berlin, 423 pp.

Maki, T. 1935. A study of the musculature of the phasmid *Megacrania tsudai* Shiraki. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University*, **12**, 1–279.

Maki, T. 1938. Studies on the thoracic musculature of insects. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University*, **24**, 1–343.

Martin, J. F. 1916. The thoracic and cervical sclerites of insects. *Annals of the Entomological Society of America*, **9**, 35–83.

Maskell, F. G. 1927. The anatomy of *Hemideina thoracica*. *Transactions of the Royal Society of New Zealand*, **57**, 637–669.

Mason, A. C. 1991. Hearing in a primitive ensiferan: the auditory system of *Cyphoderris monstrosa* (Orthoptera: Haglidae). *Journal of Comparative Physiology A*, **168**, 351–363.

Mason, A. C. 1996. Territoriality and the function of song in the primitive acoustic insect *Cyphoderris monstrosa* (Orthoptera: Haglidae). *Animal Behaviour*, **51**, 211–224.

Mason, J. B. 1961. Stridulatory mechanism in the family Schizodactylidae (Orth. Gryllacridoidea). *Eos*, **37**, 505–508.

Matsuda, R. 1956a. Morphology of the thoracic exoskeleton and musculature of a mayfly *Siphlonurus columbianus* McDunnogh (Siphlonuridae, Ephemeroptera), a contribution to the subcoxal theory of the insect thorax. *Journal of the Kansas Entomological Society*, **29**, 92–113.

Matsuda, R. 1956b. The comparative morphology of the thorax of two species of insects. *Microentomology*, **21**, 1–65.

Matsuda, R. 1970. Morphology and evolution of the insect thorax. *Memoirs of the Entomological Society of Canada*, **76**, 1–431.

McVean, A. & Field, L. H. 1996. Communication by substratum vibration in the New Zealand tree weta, *Hemideina femorata* (Stenopelmatidae: Orthoptera). *Journal of Zoology*, **239**, 101–122.

Metscher, B. D. 2009. MicroCT for comparative morphology: simple staining methods allow high-contrast 3D imaging of diverse non-mineralized animal tissues. *BMC Physiology*, **9**, 11.

Michel, K. 1974. Das Tympanalorgan von *Gryllus bimaculatus* Degeer (Saltatoria, Gryllidae). *Zeitschrift für Morphologie der Tiere*, **77**, 285–315.

Michel, K. 1980. Die Scolopalorgane in den atympanalen Tibien von *Gryllus bimaculatus* DeGeer und *Phaeophilacris spectrum* Saussure (Gryllidae, Insecta). *Zoologische Jahrbücher. Abteilung Anatomie und Ontogenie der Tiere*, **103**, 122–132.

Mickoleit, G. 1979. Zur Thoraxmorphologie der Thysanoptera. *Zoologische Jahrbücher. Abteilung Anatomie und Ontogenie der Tiere*, **79**, 1–92.

Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, a., Mayer, C., Frandsen, P. B., Ware, J., Flouri, T., Beutel, R. G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, a. J., Aspock, U., Aspock, H., Bartel, D., Blanke, a., Berger, S., Bohm, a., Buckley, T. R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L. S., Kawahara, a. Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D. D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J. L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B. M., Schutte, K., Sekiya, K., Shimizu, S., Slipinski, a., Stamatakis, a., Song, W., Su, X., Szucsich, N.

U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M. G., Wiegmann, B. M., Wilbrandt, J., Wipfler, B., Wong, T. K. F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D. K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Xu, X., Yang, H., Wang, J., Kjer, K. M. & Zhou, X. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.

Misra, S. D. 1946. Studies on the somatic musculature of the desert locust, *Schistocerca gregaria* (Forskal). Part II. The neck and the prothorax. *Indian Journal of Entomology*, **8**, 1–29.

Misra, S. D. 1947. Studies on the somatic musculature of the desert locust, *Schistocerca gregaria* (Forskal). Part III. The pterothorax. *Indian Journal of Entomology*, **9**, 19–72.

Montealegre-Z, F., Jonsson, T., Robson-Brown, K. A., Postles, M. & Robert, D. 2012. Convergent evolution between insect and mammalian audition. *Science*, **338**, 968–971.

Morris, G. K. & Gwynne, D. T. 1978. Geographical distribution and biological observations of *Cyphoderris* (Orthoptera: Haglidae) with a description of a new species. *Psyche*, **85**, 147–167.

Morris, G. K., Mason, A. C., Wall, P. & Belwood, J. 1994. High ultrasonic and tremulation signals in neotropical katydids (Orthoptera: Tettigoniidae). *Journal of Zoology*, **233**, 129–163.

Morris, G. K., De Luca, P. A., Norton, M. & Mason, A. C. 2002. Calling-song function in male haglids (Orthoptera: Haglidae, *Cyphoderris*). *Canadian Journal of Zoology*, **80**, 271–285.

Naskrecki, P. 2000. *The Phylogeny of Katydids (Insecta: Orthoptera: Tettigoniidae) and the Evolution of Their Acoustic Behaviour.* University of Conneticut, 403 pp.

Nishino, H. & Field, L. H. 2003. Somatotopic mapping of chordotonal organ neurons in a primitive ensiferan, the New Zealand tree weta *Hemideina femorata*: II. Complex tibial organ. *The Journal of Comparative Neurology*, **464**, 327–342.

O'Brien, B. & Field, L. H. 2001. Morphology and anatomy of New Zealand wetas. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CAB International, New York, 127–162.

Otte, D. 1990. The relation between hearing and flying in crickets. *Entomological News*, **101**, 29–34.

Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research*, **1**, 25–49.

Pfau, H. K. 1988. Untersuchungen zur Stridulation und Phylogenie der Gattung *Pycnogaster* Graells, 1851 (Orthoptera, Tettigoniidae, Pycnogastrinae). *Bulletin de la Société Entomologique Suisse*, **61**, 167–183.

Pfau, H. K. & Koch, U. T. 1994. The functional morphology of singing in the cricket. *The Journal of Experimental Biologyiology*, **195**, 147–167.

Rafael, J. A. & Engel, M. S. 2006. A new species of *Zorotypus* from Central Amazonia, Brazil (Zoraptera: Zorotypidae). *American Museum Novitates*, 1–11.

Ragge, D. R. 1955. *The Wing-Venation of the Orthoptera Saltatoria. With Notes on Dictyopteran Wing-Venation.* British Museum (Natural History), London, 1-159 pp.

Rähle, W. 1970. Untersuchungen am Kopf und Prothorax von *Embia ramburi* Rimsky-Korsakow 1906 (Embioptera, Embiidae). *Zoologische Jahrbücher. Abteilung Anatomie und Ontogenie der Tiere*, **87**, 248–330.

Rentz, D. C. 2010. *A Guide to the Katydids of Australia*. CSIRO Publishing, Collingwood, 214 pp.

Rentz, D. C. F. 1996. *Grasshopper Country : The Abundant Orthopteroid Insects of Australia*. University of New South Wales Press, Sydney, Australia, 284 pp.

Richards, A. M. 1955. The anatomy and morphology of the cave-orthopteran *Macropathus filifer* Walker, 1869. *Transactions of the Royal Society of New Zealand*, **83**, 405–452.

Robinson, D. J. & Hall, M. J. 2002. Sound signalling in Orthoptera. *In*: Evans, P. (ed.) *Advances in Insect Physiology*. Elsevier Ltd, 151–278.

Roff, D. A. 1994. The evolution of flightlessness: is history important? *Evolutionary Ecology*, **8**, 639–657.

Rössler, W., Jatho, M. & Kalmring, K. 2006. The auditory-vibratory sensory system in bush-crickets (Tettigoniidae, Ensifera, Orthoptera). *In*: Drosopoulos, S. & Claridge, M. (eds) *Insect Sounds and Communication: Physiology, Behaviour, Ecology and Evolution*. CRC Press, Boca Raton, London, New York, 35–69.

Sandow, J. D. & Bailey, W. J. 1978. An experimental study of defensive stridulation in *Mygalopsis ferruginea* Redtenbacher (Orthoptera: Tettigoniidae). *Animal Behaviour*, **26**, **Part 4**, 1004–1011.

Sasaki, G., Ishiwata, K., Machida, R., Miyata, T. & Su, Z.-H. 2013. Molecular phylogenetic analyses support the monophyly of Hexapoda and suggest the paraphyly of Entognatha. *BMC Evolutionary Biology*, **13**, 236.

Schmidt, A. K. & Römer, H. 2013. Diversity of acoustic tracheal system and its role for directional hearing in crickets. *Frontiers in Zoology*, **10**, 61.

Sereno, P. C. 2007. Logical basis for morphological characters in phylogenetics. *Cladistics*, **23**, 565–587.

Sharov, A. G. 1968. Phylogeny of the Orthopteroidea. *Transactions of the Institute of Paleontology. Academy of Sciences of the USSR*, **118**, 1–251.

Simmons, L. 1986. Inter-male competition and mating success in the field tricket, *Gryllus bimaculatus* (Degeer). *Animal Behaviour*, **34**, 567–579.

Simon, S. & Hadrys, H. 2013. A comparative analysis of complete mitochondrial genomes among Hexapoda. *Molecular Phylogenetics and Evolution*, **69**, 393–403.

Sismondo, E. 1980. Physical characteristics of the drumming of *Meconema thalassinum*. *Journal of Insect Physiology*, **26**, 209–212.

Snodgrass, R. E. 1929. The thoracic mechanism of a grasshopper, and its antecedents. *Smithsonian Miscellaneous Collections*, **82**, 1–111.

Snodgrass, R. E. 1935. *Principles of Insect Morphology*. 1993rd ed. McGraw-Hill, Inc., New York, London, 1-667 pp.

Song, H., Am, C., Marta, M., Desutter-, L., Heads, S. W., Huang, Y., Otte, D. & Whiting, M. F. 2015. 300 million years of diversification: elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics*, **31**, 621–651.

Song, N., Li, H., Song, F. & Cai, W. 2016. Molecular phylogeny of Polyneoptera (Insecta) inferred from expanded mitogenomic data. *Scientific Reports*, **6**, 36175.

Storch, R. H. 1968. The adult cervicothoracic musculature of the cockroach, *Nauphoeta cinerea* (Olivier). *Journal of Morphology*, **126**, 107–122.

Strauß, J. & Lakes-Harlan, R. 2008a. Neuroanatomy and physiology of the complex tibial organ of an atympanate ensiferan, *Ametrus tibialis* (Brunner von Wattenwyl, 1888) (Gryllacrididae, Orthoptera) and evolutionary implications. *Brain, Behavior and Evolution*, **71**, 167–180.

Strauß, J. & Lakes-Harlan, R. 2008b. Neuroanatomy of the complex tibial organ of *Stenopelmatus* (Orthoptera: Ensifera: Stenopelmatidae). *The Journal of Comparative Neurology*, **511**, 81–91.

Strauß, J. & Lakes-Harlan, R. 2009. The evolutionary origin of auditory receptors in Tettigonioidea: the complex tibial organ of Schizodactylidae. *Naturwissenschaften*, **96**, 143–146.

Strauß, J. & Lakes-Harlan, R. 2010. Neuroanatomy of the complex tibial organ in the splay-footed cricket *Comicus calcaris* Irish 1986 (Orthoptera: Ensifera: Schizodactylidae). *The Journal of Comparative Neurology*, **518**, 4567–4580.

Strauß, J. & Lakes-Harlan, R. 2013. Sensory neuroanatomy of stick insects highlights the evolutionary diversity of the orthopteroid subgenual organ complex. *Journal of Comparative Neurology*, **521**, 3791–3803.

Strauß, J. & Stumpner, A. 2015. Selective forces on origin, adaptation and reduction of tympanal ears in insects. *Journal of Comparative Physiology A*, **201**, 155–169.

Strauß, J., Lehmann, A. W. & Lehmann, G. U. C. 2014a. Sensory evolution of hearing in tettigoniids with differing communication systems. *Journal of Evolutionary Biology*, **27**, 200–213.

Strauß, J., Stritih, N. & Lakes-Harlan, R. 2014b. The subgenual organ complex in the cave cricket *Troglophilus neglectus* (Orthoptera: Rhaphidophoridae): comparative innervation and sensory evolution. *Royal Society Open Science*, **1**, 140240.

Strauß, J., Riesterer, A. S. & Lakes-Harlan, R. 2016. How many mechanosensory organs in the bushcricket leg? Neuroanatomy of the scolopidial accessory organ in Tettigoniidae (Insecta: Orthoptera). *Arthropod Structure and Development*, **45**, 31–41.

Stringer, I. A. N. 2006. *Distinguishing Mercury Islands Tusked Weta,* Motuweta isolata*, from a Ground Weta,* Hemiandrus pallitarsis *(Orthoptera: Anostostomatidae) in the Field, with Observations of Their Activity*. Department of Conservation, Wellington, 27 pp.

Stritih, N. & Čokl, A. 2012. Mating behaviour and vibratory signalling in non-hearing cave crickets reflect primitive communication of Ensifera. *PloS ONE*, **7**, e47646.

Stritih, N. & Stumpner, A. 2009. Vibratory interneurons in the non-hearing cave cricket indicate evolutionary origin of sound processing elements in Ensifera. *Zoology*, **112**, 48–68.

Taylor-Smith, B., Trewick, S. & Morgan-Richards, M. 2016. Three new ground wētā species and a redescription of *Hemiandrus maculifrons*. *New Zealand Journal of Zoology*, **43**, 1–21.

Terry, M. D. & Whiting, M. F. 2005. Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics*, **21**, 240–257.

Thomas, J. G. 1952. A comparison of the pterothoracic skeleton and flight muscles of male and female *Lamarckiana* species (Orthoptera, Acrididae). *Proceedings of the Zoological Society of London*, **27**, 1–12.

Tilgner, E. H. 2002. *Systematics of Phasmida*. University of Georgia, 1-113 pp.

Tilgner, E. H., Kiselyova, T. G. & McHugh, J. V. 1999. A morphological study of *Timema cristinae* Vickery with implications for the phylogenetics of Phasmida. *Deutsche Entomologische Zeitschrift*, **46**, 149–162.

Tinkham, E. R. & Rentz, D. C. F. 1969. Notes on the bionomics and distribution of the genus *Stenopelmatus* in central California with the description of a new species (Orthoptera: Gryllacrididae). *Pan-Pacific Entomologist*, **45**, 4–14.

Trautwein, M. D., Wiegmann, B. M., Beutel, R., Kjer, K. M. & Yeates, D. K. 2012. Advances in insect phylogeny at the dawn of the postgenomic era. *Annual Review of Entomology*, **57**, 449–68.

Vilhelmsen, L. 2000. Before the wasp-waist: comparative anatomy and phylogenetic implications of the skeleto-musculature of the thoraco-abdominal boundary region in basal Hymenoptera (Insecta). *Zoomorphology*, **119**, 185–221.

Vilhelmsen, L., Mikó, I. & Krogmann, L. 2010. Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society*, **159**, 22–194.

Virant-Doberlet, M. & Cockl, A. 2004. Vibrational communication in insects. *Neotropical Entomology*, **33**, 121–134.

Voss, F. 1905a. Über den Thorax von *Gryllus domesticus*. Erster Teil. Das Skelett. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (2)**, 268–514.

Voss, F. 1905b. Über den Thorax von *Gryllus domesticus*. Dritter Teil. Die Mechanik. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 645–696.

Voss, F. 1905c. Über den Thorax von *Gryllus domesticus*. Zweiter Teil. Die Muskulatur. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 355–521.

Voss, F. 1905d. Über den Thorax von *Gryllus domesticus*. Vierter Teil. Vergleich der Orthopteren, besonders des *Gryllus domesticus* mit den übrigen höheren Insektenordnungen. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 697–740.

Voss, F. 1912. Über den Thorax von *Gryllus domesticus*. Fünfter Teil. Die nachembryonale Metamorphose im ersten Stadium. *Zeitschrift für Wissenschaftliche Zoologie*, **101**, 579–682.

Walker, E. M. 1938. On the anatomy of *Gylloblatta campodeiformis* Walker. 3. Exoskeleton and musculature of the neck and thorax. *Annals of the Entomological Society of America*, **31**, 588–640.

Wang, Y., Engel, M. S., Rafael, J. A., Dang, K., Wu, H., Wang, Y., Xie, Q. & Bu, W. 2013. A unique box in 28S rRNA is shared by the enigmatic insect order Zoraptera and Dictyoptera. *PLoS ONE*, **8**.

Weber, H. 1933. *Lehrbuch Der Entomologie*. Gustav Fischer Verlag, Jena, 726 pp.

Weidner, H. 1970a. Isoptera (Termiten). *In*: Helmcke, J., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–147.

Weidner, H. 1970b. Zoraptera (Bodenläuse). *In*: Helmcke, J., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–12.

Weissmann, D. B. 2001. Communication and reproductive behaviour in North American Jerusalem crickets (*Stenopelmatus*) (Orthoptera: Stenopelmatidae). *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 351–373.

Weissmann, M. J. 1997. Natural history of the giant sand treader camel cricket, *Daihinibaenetes giganteus* Tinkham (Orthoptera: Rhaphidophoridae). *Journal of Orthoptera Research*, **6**, 33–48.

Whitfield, J. B. & Kjer, K. M. 2008. Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annual Review of Entomology*, **53**, 449–472.

Whiting, M. F., Carpenter, J. C., Wheeler, Q. D. & Wheeler, W. C. 1997. The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. *Systematic Biology*, **46**, 1–68.

Wieland, F. 2002. *Morphologische Untersuchungen am Prothorax der Mantodea (Gottesanbeterinnen)*. Göttingen, 1-90 pp.

Wieland, F. 2006. The cervical sclerites of Mantodea discussed in the context of dictyopteran phylogeny (Insecta: Dictyoptera). *Entomologische Abhandlungen*, **63**, 51–76.

Wieland, F. 2013. The phylogenetic system of Mantodea (Insecta: Dictyoptera). *Species, Phylogeny and Evolution*, **3**, 3–222.

Willemse, C. 1963. A new genus and a new species of Orthoptera from Australia. *Entomologische Berichten Amsterdam*, **23**, 1–4.

Willkommen, J. 2008. The morphology of the pterothorax of Ephemeroptera, Odonata and Plecoptera (Insecta) and the homology of wing base sclerites and flight muscles. *Stuttgarter Beiträge zur Naturkunde A*, **Neue Serie**, 203–300.

Willkommen, J. & Hörnschemeyer, T. 2007. The homology of wing base sclerites and flight muscles in Ephemeroptera and Neoptera and the morphology of the pterothorax of *Habroleptoides confusa* (Insecta: Ephemeroptera: Leptophlebiidae). *Arthropod Structure & Development*, **36**, 253–269.

Wipfler, B., Machida, R., Müller, B. & Beutel, R. G. 2011. On the head morphology of Grylloblattodea (Insecta) and the systematic position of the order, with a new nomenclature for the head muscles of Dicondylia. *Systematic Entomology*, **36**, 241–266.

Wipfler, B., Klug, R., Ge, S.-Q., Bai, M., Göbbels, J., Yang, X.-K. & Hörnschemeyer, T. 2015. The thorax of Mantophasmatodea, the morphology of flightlessness, and the evolution of the neopteran insects. *Cladistics*, **31**, 50–70.

Wittig, G. 1955. Untersuchungen am Thorax von *Perla abdominalis* Burm. (Larve und Imago) unter besonderer Berücksichtigung des peripheren Nervensystems und der Sinnesorgane. *Zoologische Jahrbücher. Abteilung Anatomie und Ontogenie der Tiere*, **74**, 491–570.

Yack, J. E. 2004. The structure and function of auditory chordotonal organs in insects. *Microscopy Research and Technique*, **63**, 315–337.

Yager, D. D. 1999. Structure, development, and evolution of insect auditory systems. *Microscopy Research and Technique*, **47**, 380–400.

Yeates, D. K., Cameron, S. L. & Trautwein, M. 2012. A view from the edge of the forest: recent progress in understanding the relationships of the insect orders. *Australian Journal of Entomology*, **51**, 79–87.

Yoshizawa, K. 2011. Monophyletic Polyneoptera recovered by wing base structure. *Systematic Entomology*, **36**, 377–394.

Yoshizawa, K. & Johnson, K. P. 2005. Aligned 18S for Zoraptera (Insecta): Phylogenetic position and molecular evolution. *Molecular Phylogenetics and Evolution*, **37**, 572–580.

Yoshizawa, K. & Saigusa, T. 2001. Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera) based on forewing base structure, with comments on monophyly of Auchenorrhyncha (Hemiptera). *Systematic Entomology*, **26**, 1–13.

Zechner, L., Hausl-Hofstätter, U. & Paill, W. 1999. Erste Nachweise von Pfaendlers Grabschrecke, *Xya pfaendleri* (Harz, 1970) in der Steiermark (Saltatoria). *Joannea Zoologie*, **1**, 79–90.

Zeuner, F. E. 1939. *Fossil Orthoptera Ensifera*. British Museum (Natural History), London, 321 pp.

Zhang, H.-L., Huang, Y., Lin, L.-L., Wang, X.-Y. & Zheng, Z.-M. 2013. The phylogeny of the Orthoptera (Insecta) as deduced from mitogenomic gene sequences. *Zoological Studies*, **52**, 37.

Zhou, Z., Shi, F. & Zhao, L. 2014. The first mitochondrial genome for the superfamily Hagloidea and implications for its systematic status in Ensifera. *PloS ONE*, **9**, e86027.

Zhou, Z., Zhao, L., Liu, N., Guo, H., Guan, B., Di, J. & Shi, F. 2017. Towards a higher-level Ensifera phylogeny inferred from mitogenome sequences. *Molecular Phylogenetics and Evolution*, **108**, 22–33.

Zwick, P. 1980. Plecoptera (Steinfliegen). *In*: Helmcke, J.-G., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–113.

Acknowledgements

I thank Benjamin Wipfler (Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-University Jena, Germany), Jana Willkommen (Zoological Institute, Dept. Functional Morphology and Biomechanics, Christian-Albrechts-University Kiel, Germany), Peter Michalik (Zoologisches Institut, Dept. Allgemeine und Systematische Zoologie mit Zoologischem Museum, Ernst-Moritz-Arndt-University Greifswald , Germany) and Susanne Düngelhoef (Zoological Research Museum Alexander Koenig Bonn, Germany) for providing µCT- or SRµCT-scans respectively.

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study.

				PROTHORAX							
taxon		species	literature	Idlm1	Idlm2	Idlm3	Idlm4	Idlm5	Idlm6	Idvm1	Idvm2
Ensifera	Gryllidae	*Gryllus campestris*	Carpentier 1923	?	?	?	?	?	?	?	?
		Acheta domesticus	Voss 1905a, b, c; 1912	0dlm2	0dlm1	0dlm1α	-	Idlm3α, β	-	0dvmδ	0dvmγ
		Gryllus bimaculatus	present study	+	+	+	-	+ (2x)	-	+	+
		*Brachytrupes portentosus**	Maki 1938	1	3	-	-	2?	-	6	8
	Gryllotalpidae	*Gryllotalpa gryllotalpa*	Carpentier 1923	?	?	?	?	?	?	?	?
		Gryllotalpa gryllotalpa	La Greca 1938	OC–NT_2	OC–NT_1	NT–NT^{I}_1	-	NT–NT^{III}_1	NT–NT^{IV}, NT–NT^{V}	OC–IU^{II}	OC–IU^{I}
	Rhaphidophoridae	*Troglophilus neglectus*	Leubner *et al.* 2016	+	-	+	-	+	-	+	+
		Diestrammena asynamora	Carpentier 1923	?	?	?	?	?	?	?	?
	Gryllacrididae	*Prosopogryllacris* sp.	present study	+	+	+	-	+	+	+	+
	Schizodactylidae	*Comicus calcaris*	Leubner *et al.* 2017	+	+	-	-	+	+	?	+
	Tettigoniidae	*Xiphidion maculatum**	Maki 1938	1	5	-	4	2	3	7	9
		Tettigonia viridissima	present study	+	+	-	+	+	+	+	+
		Conocephalus dorsalis	present study	+	+	-	+	+	+	+	+
		Pholidoptera griseoaptera	present study	+	+	-	+	+	+	+	+
		Meconema thallassinum	present study	+	+	-	+	+	+	+	+
		Meconema meridionale	present study	+	+	-	+	+	+	+	+
	Prophalangopsidae	*Cyphoderris monstrosa*	present study	+	+	-	-	+	+	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	Idvm3	Idvm4	Idvm5	Idvm6	characteristics of Idvm6	Idvm7	Idvm8	Idvm9	Idvm10	Idvm11	Idvm12	Idvm13	Idvm14
Gryllus campestris	?	?	?	?	?	?	?	?	?	?	?	ti-nt2	?
Acheta domesticus	0dvmβ	0dvmα, α'	0ism	0ism2	single	-	-	-	Iism	-	-	Idvm1 (1905b) Idvm6 (1912)	-
Gryllus bimaculatus	+	+	+	+	single	-	-	-	+	-	-	+	-
*Brachytrupes portentosus**	8	11, 12	9	10	single	-	-	-	13	-	-	16	-
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?	ti-nt2	-
Gryllotalpa gryllotalpa	OC–IU^{I}	IU–EP	IU–NT^{II}	IU–NT^{I}	single	-	-	-	NT–FU$_{2,1}$	-	-	TI–NT$^{II}_{1}$	-
Troglophilus neglectus	+	-	+	-	n.a.	-	-	-	+	-	-	+	-
Diestrammena asynamora	?	?	?	?	?	?	?	?	?	?	?	?	?
Prosopogryllacris sp.	+	-	+	+	two bundles	-	-	-	+	-	-	+ (2Bdl)	-
Comicus calcaris	?	+?	-	-	n.a.	-	-	+	+	-	-	+	-
*Xiphidion maculatum**	10	-	11?	12	single	-	-	-	13	-	-	15	-
Tettigonia viridissima	+	+	+	+	single	-	-	-	+	-	-	+	-
Conocephalus dorsalis	+	-	+	+	single	-	-	-	+	-	-	+	-
Pholidoptera griseoaptera	+	-	+	+	single	-	-	-	+	-	-	+	-
Meconema thallassinum	+	-	+	+	single	-	-	(+)	+	-	-	+	-
Meconema meridionale	+	-	+	+	single	-	-	(+)	+	-	-	+	-
Cyphoderris monstrosa	+	-	+	+	single	-	-	+	+	-	-	+	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ldvm15	ldvm16	ldvm17	ldvm18	ldvm19	characteristics of ldvm19	ltpm1	ltpm2	ltpm2-2	ltpm3	ltpm4
Gryllus campestris	?	cx-nt2	cx-nt3	cx-nt4	tr-nt3, tr-nt4	one bundle running behind cryptopleura	-	?	?	?	?
Acheta domesticus	-	ldvm2	ldvm7	lpm6	ldvm8, lpm6α	one bundle running behind cryptopleura	-	0vlm5α	0idvm1, 2	-	lpm9, 11, 12
Gryllus bimaculatus	-	+	+	+	+ (2 Bdl)	one bundle running behind cryptopleura	-	+ (1x)	+	-	+ (3x)
*Brachytrupes portentosus**	-	19	20	21	27, 30	one bundle running behind cryptopleura	-	14	- (?)	-	- (?)
Gryllotalpa gryllotalpa	cx-nt1	cx-nt2	cx-nt3, cx-em1	cx-nt4, cx-em2	tr-nt4, tr-em	two bundles	-	?	?	?	?
Gryllotalpa gryllotalpa	$CX–NT^{VI}{}_1$	$CX–NT^{I}{}_1$, $CX–NT^{II}{}_1$, CX–EM	$CX–NT^{III}{}_1$, CX–AM	$CX–NT^{IV}{}_1$	$TR–NT_1$, $TR–EM^{III}$	two bundles	-	OC–EM	OC–EP	-	-
Troglophilus neglectus	-	+	?	+	+	single	-	-	-	-	-
Diestrammena asynamora	?	?	?	?	?	?	-	?	?	?	?
Prosopogryllacris sp.	-	+	+	+	+	single	-	+	-	-	-
Comicus calcaris	-	+	+	+	+	single	-	+ (2x)	-	-	-
*Xiphidion maculatum**	-	18	19	20	25	single	-	?	-	-	-
Tettigonia viridissima	-	+	+	+	+	single	-	+	-	-	-
Conocephalus dorsalis	-	+	+	+	+	single	-	+	-	-	-
Pholidoptera griseoaptera	-	+	+	+	+	single	-	+	-	-	-
Meconema thallassinum	-	+	+	+	+	single	-	+	-	-	-
Meconema meridionale	-	+	+	+	+	single	-	+	-	-	-
Cyphoderris monstrosa	-	+	+	+	+	single	-	+	-	-	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ltpm5	ltpm6	ltpm7	lspm1	lspm2	origin of lspm2	lspm3	lspm4	lspm5	lspm6	lspm7	lpcm1	lpcm2	lpcm3	lpcm4	lpcm5
Gryllus campestris	?	?	?	?	?	?	?	?	?	?	?	?	?	ti-es3	cx-es1	?
Acheta domesticus	- ?	-	-	lzm	-	n.a.	-	-	-	-	-	-	0vlm2	lpm5	lpm4	-
Gryllus bimaculatus	-	-	-	(+)	-	n.a.	-	-	-	-	-	-	+	+	+	-
*Brachytrupes portentosus**	-	-	-	15	-	n.a.	-	-	-	-	-	-	17	25	26	-
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?	-	?	-	cx-es1	-
Gryllotalpa gryllotalpa	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	$CX–EP^{l}_{1}$	-
Troglophilus neglectus	-	-	-	-	-	n.a.	-	-	+	-	-	-	+	+	+	+
Diestrammena asynamora	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Prosopogryllacris sp.	-	-	-	+	-	n.a.	-	-	-	-	-	-	-	+	+	+
Comicus calcaris	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	+	+	+
*Xiphidion maculatum**	-	-	-	14	34	laterally on spinasternite	-	-	-	-	-	-	16	?	23	24
Tettigonia viridissima	-	-	-	+	+	laterally on spinasternite	-	-	-	-	-	-	+	+	+	+
Conocephalus dorsalis	-	-	-	+	+	laterally on spinasternite	-	-	-	-	-	-	+	+	+	+
Pholidoptera griseoaptera	-	-	-	+	+	laterally on spinasternite	-	-	-	-	-	-	+	+	+	+
Meconema thallassinum	-	-	-	+	+	laterally on spinasternite	-	-	-	-	-	-	+	+	+	+
Meconema meridionale	-	-	-	+	+	laterally on spinasternite	-	-	-	-	-	-	+	+	+	+
Cyphoderris monstrosa	-	-	-	?	-	n.a.	-	-	-	-	-	-	+	+	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	lpcm6	lpcm7	lpcm8	lvlm1	lvlm2	lvlm3	lvlm4	lvlm5	lvlm6	lvlm7	lvlm8	lvlm8 paired, unpaired	lvlm9
Gryllus campestris	?	?	tr-es a+b	?	?	?	?	?	?	?	?	?	?
Acheta domesticus	-	-	lpm4α, ldvm5	-	-	0vlm3, 4, 5	lvlm7	-	lvlm6	lvlm4, 5	lvlm1	unpaired	lvlm3
Gryllus bimaculatus	-	-	+ (2 Bdl)	-	-	+ (2x)	+	-	+	+ (2x)	+	unpaired	+ (2x)
*Brachytrupes portentosus**	-	-	28, 29	-	-	4, 5	7	-	36	34	35	unpaired	37
Gryllotalpa gryllotalpa	-	-	tr-es, tr-em	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	-	-	TR–EP_1, TR–EM^I, TR–EM^{II}	-	-	TN–FU	SP–FU^I_1, SP–FU^{II}_1	-	SP–$FU_{2,1}$	FU–$FU^I_{2,1}$, FU–$FU^{II}_{2,1}$, FU–$FU^{III}_{2,1}$, FU–$FU^{IV}_{2,1}$	SP–SP	unpaired	FU–$SP^I_{2,1}$, FU–$SP^{II}_{2,1}$
Troglophilus neglectus	-	-	+ (2Bdl)	-	-	+	+	-	+	+	+	paired	+
Diestrammena asynamora	?	?	?	?	?	?	?	?	?	?	?	?	?
Prosopogryllacris sp.	-	-	+ (2Bdl)	-	-	+	+	-	+	+ (2x)	+	paired	+
Comicus calcaris	-	-	+ (2Bdl)	-	-	+	+	-	+	+ (2x)	-	n.a.	-
*Xiphidion maculatum**	-	-	26, 27	-	-	6	8	-	- (?)	31	32	?	33
Tettigonia viridissima	-	-	+ (2Bdl)	-	-	+	+	-	+	+	+	paired	+
Conocephalus dorsalis	-	-	+ (2Bdl)	-	-	+	+	-	+	+	+	paired	+
Pholidoptera griseoaptera	-	-	+ (2Bdl)	-	-	+	+	-	+	+	+	paired	+
Meconema thallassinum	-	-	+ (2Bdl)	-	-	+	+	-	+	+	+	paired	+
Meconema meridionale	-	-	+ (2Bdl)	-	-	+	+	-	+	+	+	paired	+
Cyphoderris monstrosa	-	-	+ (2Bdl)	-	-	+	+	-	+	+	+	paired	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

		MESOTHORAX								
species	Ivlm10	Iscm1	Iscm2	Iscm3	Iscm4	Iscm5	Iscm6	Iscm7	IIdlm1	IIdlm2
Gryllus campestris	?	?	?	?	?	?	?	?	?	?
Acheta domesticus	-	Ibm1	Ibm2	Ibm3	-	Ibm7	Ibm4	Ivlm2	IIdlm1, 2	IIdlm3, 4
Gryllus bimaculatus	-	+	+	+	-	+	+	+	+ (1x)	+ (2x)
*Brachytrupes portentosus**	-	18	23	24	-	22	31	46	32	33
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	-	TI–FU	CX–FU^{I}_{1}	CX–FU^{I}_{1}	-	-	-	-	$NT–NT^{I}_{2}$	$NT–NT^{III}_{2}$
Troglophilus neglectus	-	+ (3x)	+	+	-	+	-	+	+	-
Diestrammena asynamora	?	?	?	?	?	?	?	?	?	?
Prosopogryllacris sp.	-	+	+	+	-	+	+	+	+	+ (2x)
Comicus calcaris	-	+	+	+	+	-	-	-	+	-
*Xiphidion maculatum**	-	17	21	22	-	?	28?	43	29	30
Tettigonia viridissima	-	+	+	+	-	+	-	+	+	+ (4x)
Conocephalus dorsalis	-	+	+	+	-	+	-	+	+	+ (3x)
Pholidoptera griseoaptera	-	+	+	+	-	+	-	+	+	+
Meconema thallassinum	-	+	+	+	-	+	-	+	+	+
Meconema meridionale	-	+	+	+	-	+	-	+	+	+
Cyphoderris monstrosa	-	+	+	+	-	+	-	+	+	+ (2x)

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIdvm1	characteristics of IIdvm1	IIdvm2	IIdvm3	IIdvm4	IIdvm5	IIdvm6	IIdvm7	IIdvm8	IIdvm9	IItpm1
Gryllus campestris	Is-nt2	single	ti-nt1, ti-nt2	-	cx-nt2	cx-nt3	cx-em2	tr-nt1, tr-nt2	?	?	?
Acheta domesticus	IIdvm7	single	IIdvm1, 6	-	IIdvm3, 4	IIdvm2	IIpm6	IIdvm5	IIism	-	IIpm10
Gryllus bimaculatus	+	single	+ (1x)	-	+	+	+	+	+	-	-
*Brachytrupes portentosus**	38	single	44	-	48	49	50	57	39	-	-
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	-	n.a.	$TI–NT^{I}_{2}$, $TI–NT^{II}_{2}$	-	$CX–NT^{IV}_{2}$	$CX–NT^{III}_{2}$	$A–CX_{2}$	$TR–NT_{2}$	$NT–FU_{3,2}$	-	-
Troglophilus neglectus	-	n.a.	?	-	+	+	+	+	-	-	-
Diestrammena asynamora	-	n.a.	ti-nt1, ti-nt2	-	cx-nt2	cx-nt3	cx-em2	tr-nt1, tr-nt2	?	?	?
Prosopogryllacris sp.	-	n.a.	+	-	+	+	+	+	+	-	+
Comicus calcaris	-	n.a.	-	-	+	+	+	+	+	-	-
*Xiphidion maculatum**	36	single	41	-	45	46	47	54	-	-	?
Tettigonia viridissima	+	single	+	-	+	+	+	+	-	-	+
Conocephalus dorsalis	?	?	+	-	+	+	+	+	-	-	+
Pholidoptera griseoaptera	-	n.a.	+	-	+	+	+	+	-	-	-
Meconema thallassinum	-	n.a.	+	-	+	+	+	+	-	-	+
Meconema meridionale	-	n.a.	+	-	+	+	+	+	-	-	+
Cyphoderris monstrosa	+	single	+	-	+	+	+	+	-	-	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IItpm2	IItpm3	IItpm4	IItpm5	IItpm6	IItpm7	IItpm8	IItpm9	IItpm10	IItpm11	IItpm12	IItpm13	IIppm1
Gryllus campestris	?	?	?	?	?	?	?	?	?	?	?	-	ls-es2?
Acheta domesticus	IIpm11	-	-	IIpm9	-	-	IIpm13?	IIpm12, 13?	IIpm7	-	-	-	IIpm5d, e
Gryllus bimaculatus	+	-	-	+	-	-	+ (?)	+ (1x)	-	-	-	-	+
*Brachytrupes portentosus**	40	-	-	- (?)	-	-	- (?)	41	-	-	-	-	?
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	PFL–NT_2	-	-	FL–NT_2 ?	-	-	A–FL_2 ?	A–APP_2	EM–EM_2	-	-	-	LS–EP_2
Troglophilus neglectus	-	-	-	-	-	-	-	-	+	-	-	-	-
Diestrammena asynamora	?	?	?	?	?	?	?	?	?	?	?	?	?
Prosopogryllacris sp.	+	-	-	-	-	-	+	+	+	-	-	-	+
Comicus calcaris	-	-	-	-	-	-	-	-	-	-	-	-	+ (?)
*Xiphidion maculatum**	37	-	-	38	-	-	?	39	?	-	-	-	?
Tettigonia viridissima	+	-	-	+	-	-	+	+	+	-	-	-	+
Conocephalus dorsalis	+	-	-	?	-	-	+	+	+	-	-	-	+
Pholidoptera griseoaptera	-	-	-	-	-	-	-	+	+	-	-	-	+
Meconema thallassinum	+	-	-	-	-	-	+	+	+	-	-	-	+
Meconema meridionale	+	-	-	-	-	-	+	+	+	-	-	-	+
Cyphoderris monstrosa	-	-	-	+	-	-	+	+	+	-	-	-	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIppm2	IIspm1	IIspm2	IIspm3	IIspm4	IIspm5	IIspm6	IIspm7	IIspm8	IIspm9	IIpcm1	IIpcm2	IIpcm3
Gryllus campestris	-	ls-es1	?	?	?	?	?	?	?	?	ti-es3	ti-es1, ti-es2	cx-es1, cx-es2
Acheta domesticus	-	IIpm14	IIzm	IIifm	-	-	-	-	-	-	IIpm1	IIpm2, IIpm5b+c	IIpm4, IIpm5a
Gryllus bimaculatus	-	?	+	+	-	-	-	-	-	-	+	+	+
*Brachytrupes portentosus**	-	42	43	65	-	-	-	-	-	-	56	45	54, 55
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	-	-	-	SP–PR	-	-	-	-	-	-	TI–EP^{I}_{2}	TI–EP^{I}_{2}, TI–EP^{III}_{2}	CX–EP^{II}_{2}
Troglophilus neglectus	-	-	+	-	-	-	+	-	-	+	+	+	+
Diestrammena asynamora	?	?	?	?	?	?	?	?	?	?	ti-es3	ti-es2	cx-es1, cx-es2
Prosopogryllacris sp.	-	-	+	+	-	-	-	-	-	-	+	+	+
Comicus calcaris	-	-	+	-	-	-	-	-	-	-	+	+	+
*Xiphidion maculatum**	-	-	40	61	-	-	-	-	-	-	53	42	51
Tettigonia viridissima	-	-	+	+	-	-	-	-	-	-	+	+	+
Conocephalus dorsalis	-	-	+	+	-	-	-	-	-	-	+	+	+
Pholidoptera griseoaptera	-	-	+	+	-	-	-	-	-	-	+	+	+
Meconema thallassinum	-	-	+	+	-	-	-	-	-	-	+	+	+
Meconema meridionale	-	-	+	+	-	-	-	-	-	-	+	+	+
Cyphoderris monstrosa	-	+?	+	+	-	-	-	-	-	-	+	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIpcm4	IIpcm5	IIpcm6	IIvlm1	IIvlm2	IIvlm3	characteristics of IIvlm3	IIvlm4	IIvlm5	IIvlm6	IIvlm7	IIscm1	IIscm2	IIscm3
Gryllus campestris	cx-es1	tr-es	?	?	?	?		?	?	?	?	?	?	?
Acheta domesticus	IIpm5a	IIpm3	-	-	-	IIvlm4, 5	distinct muscle	-	IIvlm3	-	-	IIbm1 (3teilig)	IIbm2?	IIbm3, 6
Gryllus bimaculatus	+	+	-	-	-	+ (2x)	distinct muscle	-	+	-	-	+ (3x)	-	+
*Brachytrupes portentosus**	55	58	-	-	-	63	distinct muscle	-	64	-	-	47	-	53
Gryllotalpa gryllotalpa	?	?	?	?	?	?		?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	CX–EP^{I}_{2}	TR–EP_{2}	-	-	-	FU–$FU^{I}_{3,2}$	distinct muscle	-	FU–$SP^{II}_{3,2}$	-	-	CX–FU^{I}_{2}, CX–FU^{IV}_{2}	-	CX–FU^{II}_{2}
Troglophilus neglectus	+	+	-	-	-	+	distinct muscle	-	+	-	-	+ (2x)	-	+
Diestrammena asynamora	cx-es1	tr-es	-	?	?	?		?	?	?	?	?	?	?
Prosopogryllacris sp.	+	+	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
Comicus calcaris	+	+	-	-	-	+	distinct muscle	-	+	-	-	+ (2x)	-	+
*Xiphidion maculatum**	52	55	-	35 (?)	-	59	distinct muscle	-	60	-	-	44	-	50
Tettigonia viridissima	+	+	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
Conocephalus dorsalis	+	+	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
Pholidoptera griseoaptera	+	+	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
Meconema thallassinum	+	+	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
Meconema meridionale	+	+	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
Cyphoderris monstrosa	+	+	-	-	-	+	distinct muscle	-	+	-	-	+ (2x)	-	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

	METATHORAX										
species	IIscm4	IIscm5	IIscm6	IIscm7	IIIdlm1	IIIdlm2	IIIdvm1	IIIdvm2	IIIdvm3	IIIdvm4	IIIdvm5
Gryllus campestris	?	?	?	?	?	?	?	ti-nt1, ti-nt2	-	cx-nt2	cx-nt3
Acheta domesticus	IIbm5	IIbm7	IIbm4	IIvlm2	IIIdlm1	IIIdlm1α, 3, 4	-	IIIdvm1, 6	-	IIIdvm3, 4	IIIdvm2
Gryllus bimaculatus	+	+	+	+	+	?	-	+	-	+	+
*Brachytrupes portentosus**	52	51	59	74	62	-	-	71, 72	-	76	77
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	CX–FU^{III}_2, CX–FU^{V}_2	CX–SP^{I}_2, CX–SP^{II}_2	TR–FU_2	CX–$SP_{3,2}$	NT–NT^{I}_3, NT–NT^{II}_3	NT–NT^{III}_3	-	TI–NT^{I}_3, TI–NT^{II}_3	-	CX–NT^{IV}_3, CX–NT^{V}_3	CX–NT^{III}_3
Troglophilus neglectus	+	+	+	+	+	-	-	+	-	+	+
Diestrammena asynamora	?	?	?	?	?	?	-	ti-nt1, ti-nt2	-	cx-nt2	cx-nt3
Prosopogryllacris sp.	+	+	+	+	+	+ (2x)	-	+	-	+	+ (2Bdl)
Comicus calcaris	+	+	+	+	+	-	-	+	-	+	+
*Xiphidion maculatum**	49?	48	56	68	58	-	-	66	-	70	71
Tettigonia viridissima	+	+	+	+	+	-	-	+	-	+	+
Conocephalus dorsalis	+	+	+	+	+	-	-	+	-	+	+
Pholidoptera griseoaptera	+	+	+	+	+	-	-	+	-	+	+
Meconema thallassinum	+	+	+	+	+	+	-	+ (2Bdl)	-	+	+
Meconema meridionale	+	+	+	+	+	+	-	+ (2Bdl)	-	+	+
Cyphoderris monstrosa	+	+	+	+	+	-	-	+	-	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIIdvm6	IIIdvm7	IIIdvm8	IIItpm1	IIItpm2	IIItpm3	IIItpm4	IIItpm5	IIItpm6	IIItpm7	IIItpm8	IIItpm9
Gryllus campestris	cx-em2	tr-nt1, tr-nt2	?	?	?	?	?	?	?	?	?	?
Acheta domesticus	IIIpm6	IIIdvm5	IIIism	IIIpm10, IIIpm8?	IIIpm11	-	-	IIIpm9	-	-	-	IIIpm12
Gryllus bimaculatus	+	+	+	- ?	+	-	-	-	-	-	-	+
*Brachytrupes portentosus**	78	85	66	-	67	-	-	-	-	-	-	68
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	A–CX_3	TR–NT_3	NT–$FU_{1A,3}$	-	PFL–NT_3	-	-	FL–NT_3 ?	-	-	A–FL_3 ?	APP–NT
Troglophilus neglectus	+	+	-	-	-	-	-	-	-	-	-	-
Diestrammena asynamora	cx-em2	tr-nt1, tr-nt2	?	?	?	?	?	?	?	?	?	?
Prosopogryllacris sp.	+	+	+	+	+	-	-	-	-	-	+	+
Comicus calcaris	+	+	+	-	-	-	-	-	-	-	-	-
*Xiphidion maculatum**	72	79	?	-	62	-	-	-	-	-	?	63
Tettigonia viridissima	+	+	-	-	+	-	-	-	-	-	+	+
Conocephalus dorsalis	+	+	+	-	+	-	-	-	-	-	+	+
Pholidoptera griseoaptera	+	+	+	-	-	-	-	-	-	-	-	+
Meconema thallassinum	+	+	+	?	+	-	-	-	-	-	+	+
Meconema meridionale	+	+	+	+	+	-	-	-	-	-	+	+
Cyphoderris monstrosa	+	+	+	+	-	-	-	-	-	-	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIItpm10	IIItpm11	IIItpm12	IIItpm13	IIIppm1	IIIppm2	IIIspm1	IIIspm2	IIIspm3	IIIspm4	IIIspm5	IIIpcm1	IIIpcm2	IIIpcm3	IIIpcm4
Gryllus campestris	?	?	?	?	-	-	-	?	?	?	?	ti-es3	ti-es1, ti-es2	cx-es1, cx-es2	cx-es1
Acheta domesticus	IIIpm7	-	?	-	-	-	-	IIIzm	-	-	-	IIIpm1	IIIpm2, 5b	IIIpm4	IIIpm5a
Gryllus bimaculatus	+	-	-	-	-	-	-	+	-	-	-	?	+	+	+
*Brachytrupes portentosus**	69	-	-	-	-	-	-	70	-	-	-	84	73	82	83
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	EM–EM_3	-	-	-	-	-	-	PP–FU_3	-	-	-	TI–EP^I_3	TI–EP^{II}_3, TI–EP^{III}_3	CX–EP^I_3	CX–EP^{II}_3
Troglophilus neglectus	+	-	-	-	-	-	-	+	-	-	+	+	+	+	+
Diestrammena asynamora	?	?	?	?	?	?	?	?	?	?	?	ti-es3	ti-es2	cx-es1, cx-es2	cx-es1
Prosopogryllacris sp.	+	-	-	-	+	-	-	+	-	-	+	+	+	+	+
Comicus calcaris	-	-	-	-	+	-	-	+	-	-	+ (2x?)	+	+	+	+
*Xiphidion maculatum**	64	-	-	-	?	-	-	65	-	-	-	78	67	76	77
Tettigonia viridissima	+	-	-	-	+	-	-	+	-	-	-	+	+	+	+
Conocephalus dorsalis	+	-	-	-	+	-	-	+	-	-	-	+	+	+	+
Pholidoptera griseoaptera	+	-	-	-	+	-	-	+	-	-	-	+	+	+	+
Meconema thallassinum	+	-	-	-	+	-	-	+	-	-	-	+	+	+	+
Meconema meridionale	+	-	-	-	+	-	-	+	-	-	-	+	+	+	+
Cyphoderris monstrosa	+	-	-	-	+	-	-	+	-	-	+	+	+	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIIpcm5	IIIpcm6	IIIpcm7	IIIvlm1	IIIvlm2	IIIvlm3	IIIscm1	IIIscm2	IIIscm3	IIIscm4	IIIscm5	IIIscm6
Gryllus campestris	tr-es	?	?	?	?	?	?	?	?	?	?	?
Acheta domesticus	IIIpm3	-	-	-	IIIvlm2-5	IIIvlm1	IIIbm1	IIIbm2	IIIbm3	IIIbm5	-	IIIbm4
Gryllus bimaculatus	+	-	-	-	+	+	+	+	+	+	-	+
*Brachytrupes portentosus**	86	-	-	-	95?	94?	75	79	81	80	-	87
Gryllotalpa gryllotalpa	?	?	?	?	?	?	?	?	?	?	?	?
Gryllotalpa gryllotalpa	TR–EP_3	-	-	-	?	?	CX–FU^{I}_3	CX–FU^{VI}_3, CX–FU^{VII}_3	CX–FU^{II}_3	CX–FU^{III}_3	-	TR–FU_3
Troglophilus neglectus	+	-	-	-	-	-	+	+	+	+	-	+
Diestrammena asynamora	tr-es	-	-	?	?	?	?	?	?	?	?	?
Prosopogryllacris sp.	+	-	-	-	+	+	+	+	+	+	-	+
Comicus calcaris	+	-	-	-	-	-	+	+	+	+	-	+
*Xiphidion maculatum**	80	-	-	-	88?	85?	69	73	75	74	-	81
Tettigonia viridissima	+	-	-	-	+	+ (2x)	+ (2x)	+ (2x)	+	+	-	+
Conocephalus dorsalis	+	-	-	-	+	+	+	+ (2x)	+	+	-	+
Pholidoptera griseoaptera	+	-	-	-	+	+	+	+ (2x)	+	+	-	+
Meconema thallassinum	+	-	-	-	+	+	+	+ (2x)	+	+	-	+
Meconema meridionale	+	-	-	-	+	+	+	+ (2x)	+	+	-	+
Cyphoderris monstrosa	+	-	-	-	+	+	+	+ (2x)	+	+	-	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

				PROTHORAX							
taxon		**species**	**literature**	**ldlm1**	**ldlm2**	**ldlm3**	**ldlm4**	**ldlm5**	**ldlm6**	**ldvm1**	**ldvm2**
Ensifera	Anostostomatidae	*Papuaistus* sp.	present study	+	+	+	-	+	+	+	+
		Hemideina crassidens	present study	+	+	+	-	+	+	+	+
	Stenopelmatidae	*Stenopelmatus* sp.	present study	+	+	-	-	+	+	?	+
Caelifera	Acridiidae	*Locusta migratoria manilensis**	Maki 1938	1	5, 6	2	-	-	3 (2 Bdl), 4	11	13
		Locusta migratoria	Albrecht 1953	49	47, 48	56	-	-	58, 58a, 58b	52x	50
		Dissosteira carolina	Snodgrass 1929	49	47, 48	56	-	-	58 (several bundles)	- (?)	50
		Schistocerca gregaria	Misra 1946, 1947	52	50, 51	65	-	-	66 (4 bdls)	62	55
		Stenobothrus lineatus	present study	+	+ (2x)	+	-	-	+ (4bdl)	+	+
Caelifera	Lentulidae	*Lentula callani*	Ewer 1958	?	?	?	?	?	?	?	?
	Pamphagidae	*Lamarckiana* sp.	Thomas 1952	?	?	?	?	?	?	?	?
	Pyrgomorphidae	*Atractomorpha ambigua**	Maki 1938	1	5	2	-	-	3, 4	10	11
		Zonocerus elegans	Ewer 1954								
		Psednura sp.	Blackith & Blackith 1967	?	?	?	?	?	+ (three bundles)	?	?
	Proscopiidae	*Cephalocoema albrechti*	Zolessi 1968	-	47, 48	49	-	-	58, 58a	- (?)	50
	Eumastacidae	Different unindentified species: (P59) (P79) (P127)	Blackith & Blackith 1967	49 (P79)	47 (P79)	56 (P79)	-	-	58 (P79)	52x (P79)	50 (P79)
	Tridactylidae	*Xya* sp.	present study	+	+	+	-	-	+	+	+
Phasmatodea		*Timema nevadense*	Klug 2008	?	?	?	?	?	?	?	?

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ldvm3	ldvm4	ldvm5	ldvm6	characteristics of ldvm6	ldvm7	ldvm8	ldvm9	ldvm10	ldvm11	ldvm12	ldvm13	ldvm14
Papuaistus sp.	+	+	+	+	single	-	-	+	+	-	-	+	-
Hemideina crassidens	+	+	+	+	single	-	-	+	+	-	-	+	-
Stenopelmatus sp.	+	+	+	+	single	-	-	+	+	-	-	+	-
*Locusta migratoria manilensis**	14	-	- (?)	15, 16	duplicated	-	-	-	17	-	-	20	-
Locusta migratoria	51	-	53	52, 52a	duplicated	-	-	-	59	-	-	62, 62a	-
Dissosteira carolina	51	-	53	52a, 52b	duplicated	-	-	-	59	-	-	62	-
Schistocerca gregaria	56	-	60	57, 58, 59	duplicated	-	-	-	67	-	-	70i, ii, iii, iv	-
Stenobothrus lineatus	?	-	+	+ (2x)	duplicated	-	-	-	+	-	-	+ (2bdl)	-
Lentula callani	?	?	?	?	?	?	?	?	?	?	?	?	?
Lamarckiana sp.	?	?	?	?	?	?	?	?	?	?	?	?	?
*Atractomorpha ambigua**	12	-	-	13, 14	duplicated	-	-	-	15	-	-	17	-
Zonocerus elegans													
Psednura sp.	?	?	?	?	?	?	?	?	+	?	?	?	?
Cephalocoema albrechti	51	52x	-	52, 53	duplicated	-	-	-	59?	-	-	62	-
Different unindentified species: (P59) (P79) (P127)	51 (P79)	52c (P79)	53 (P79)	52a, 52b (P79)	duplicated	-	-	-	59 (P79)	-	-	62, 62a (P59)	-
Xya sp.	+	-	+	+	duplicated	-	-	-	+	-	-	+	-
Timema nevadense	?	?	?	?	?	?	?	?	?	?	?	?	?

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ldvm15	ldvm16	ldvm17	ldvm18	ldvm19	characteristics of ldvm19	ltpm1	ltpm2	ltpm2-2	ltpm3	ltpm4
Papuaistus sp.	-	+	+	+	+	single	-	+	-	-	-
Hemideina crassidens	-	+	+	+	+	single	-	+	-	-	-
Stenopelmatus sp.	-	+	+	+	+	single	-	+	-	-	-
*Locusta migratoria manilensis**	-	22	23	24	30	single	-	18	-	-	-
Locusta migratoria	-	63	65	64	71d	single	-	57	-	-	-
Dissosteira carolina	-	63	65	64	71d	single	-	57	-	-	-
Schistocerca gregaria	-	71i	71ii	71iii	77iii	single	-	54	-	-	-
Stenobothrus lineatus	-	+	+	+	+	single	-	+	-	-	-
Lentula callani	?	?	?	?	?	?	?	?	?	?	?
Lamarckiana sp.	?	?	?	?	?	?	?	?	?	?	?
*Atractomorpha ambigua**	-	20	21	22	27	single	-	16	-	-	-
Zonocerus elegans											
Psednura sp.	?	?	?	?	?	?	-	-	?	?	?
Cephalocoema albrechti	-	65	63	64	71d	single	-	-	-	-	-
Different unindentified species: (P59) (P79) (P127)	-	63 (P59)	65 (P59)	64 (P59)	71d (P59)	single	-	-	-	-	-
Xya sp.	-	+	+	+ (2x)	+	single	-	+	-	-	-
Timema nevadense	?	?	?	?	?	?	?	?	?	?	?

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ltpm5	ltpm6	ltpm7	lspm1	lspm2	origin of lspm2	lspm3	lspm4	lspm5	lspm6	lspm7	lpcm1	lpcm2	lpcm3	lpcm4	lpcm5
Papuaistus sp.	-	-	+	+	-	n.a.	-	-	-	-	-	-	+	+	+	+
Hemideina crassidens	-	-	+	+	-	n.a.	-	-	-	-	-	-	+	+	+	+
Stenopelmatus sp.	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	?	+	+
*Locusta migratoria manilensis**	-	-	-	19	-	n.a.	-	-	-	-	-	-	-	-	28	29
Locusta migratoria	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	68a	68
Dissosteira carolina	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	68a, 68b	?
Schistocerca gregaria	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	74i, ii	75
Stenobothrus lineatus	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	+ (2x)	+
Lentula callani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lamarckiana sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Atractomorpha ambigua**	-	-	-	(+)*	-	n.a.	-	-	-	-	-	-	-	18	26	25
Zonocerus elegans																
Psednura sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cephalocoema albrechti	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	68	68a
Different unindentified species: (P59) (P79) (P127)	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	68a, 68b (P59)	68c (P59)
Xya sp.	-	-	-	-	-	n.a.	-	-	-	-	-	-	+	-	+	+ (2x)
Timema nevadense	?	?	?	?	+	laterally on posterior margin of posterior sternal plate	?	?	?	?	?	?	?	?	?	?

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	lpcm6	lpcm7	lpcm8	lvlm1	lvlm2	lvlm3	lvlm4	lvlm5	lvlm6	lvlm7	lvlm8	lvlm8 paired, unpaired	lvlm9
Papuaistus sp.	-	-	+ (2Bdl)	-	-	+	+	-	+	+ (2x)	-	n.a.	+
Hemideina crassidens	-	-	+ (2Bdl)	-	-	+	+	-	+	+ (2x)	+	paired	+
Stenopelmatus sp.	-	-	+ (2Bdl)	-	-	+	+	-	+	+ (2x)	+	paired	+
*Locusta migratoria manilensis**	-	-	31, 32	-	-	7, 8, 9	12	-	-	37	38	?	39
Locusta migratoria	-	-	71b, 71c	-	-	55	61	-	-	60	88	paired	87
Dissosteira carolina	-	-	71b, 71c	-	-	55	61	-	-	60	88	paired	87
Schistocerca gregaria	-	-	77i, ii	-	-	53, 63	69	-	-	68	96	paired	95
Stenobothrus lineatus	-	-	+ (2x)	-	-	+	+	-	-	+	+	paired	+
Lentula callani	?	?	?	?	?	?	?	?	?	?	?	?	?
Lamarckiana sp.	?	?	?	?	?	?	?	?	?	?	?	?	?
*Atractomorpha ambigua**	-	-	28	-	-	6, 7, 8	-	-	-	32	-	n.a.	33
Zonocerus elegans													
Psednura sp.	?	?	?	?	?	?	?	?	?	?	?	?	?
Cephalocoema albrechti	-	-	71b, 71e	-	-	55, 55a	-	-	-	60	88	paired	87
Different unindentified species: (P59) (P79) (P127)	-	-	71b, 71c, 71x (P59)	-	-	55a, b, c (P127)	61 (P59)	-	-	60 (P127)	88 (P127)	paired	87 (P127)
Xya sp.	-	-	+	-	-	+	+	-	-	+	+	paired	+
Timema nevadense	?	?	?	?	?	?	?	?	+	+	?	?	?

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

								MESOTHORAX		
species	Ivlm10	Iscm1	Iscm2	Iscm3	Iscm4	Iscm5	Iscm6	Iscm7	IIdlm1	IIdlm2
Papuaistus sp.	-	+ (2x)	+	+	-	+	-	+	+	+ (2x)
Hemideina crassidens	-	+ (2x)	+	+	-	+	-	+	+	+ (2x)
Stenopelmatus sp.	-	+	+	-	-	-	-	+	+	+ (2x)
*Locusta migratoria manilensis**	10	21	-	27	-	25, 26	-	-	33	34, 35, 36
Locusta migratoria	54	-	-	69	66	67	-	-	81	- (?)
Dissosteira carolina	54	-	-	69	66	67	-	-	81	82
Schistocerca gregaria	61	-	-	-	-	72, 73	-	-	89	87, 88
Stenobothrus lineatus	+	+	-	+	+	+	-	-	+	+
Lentula callani	?	?	?	?	?	?	?	?	?	-
Lamarckiana sp.	?	?	?	?	?	?	?	?	d.l.m. (lacking in wingless female)	o.d.m.
*Atractomorpha ambigua**	9	19	-	24	-	23	29?	-	30	31
Zonocerus elegans									81	oblique dorsal muscles
Psednura sp.	+	?	?	?	?	?	?	?	?	?
Cephalocoema albrechti	-	66	-	69	69a	67	-	-	-	-
Different unindentified species: (P59) (P79) (P127)	54 (P79)	anterior rotator of the fore coxa (P59)	-	69 (P59)	66 (P59)	67 (P59)	-	87x (P127)	-	-
Xya sp.	-	-	-	+	-	-	-	-	+	-
Timema nevadense	?	?	?	?	?	?	?	+	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIdvm1	characteristics of IIdvm1	IIdvm2	IIdvm3	IIdvm4	IIdvm5	IIdvm6	IIdvm7	IIdvm8	IIdvm9	IItpm1
Papuaistus sp.	-	n.a.	+	-	+	+	+	+	+	-	-
Hemideina crassidens	-	n.a.	+	-	+	+	+	+	+	-	-
Stenopelmatus sp.	-	n.a.	+	-	+	+	+	+	+	-	-
*Locusta migratoria manilensis**	40, 41, 42	multiplicated	51, 58?	-	53	54	55	62	43	-	44
Locusta migratoria	83, 84	multiplicated	89	-	90	91	99	103b, 103c	-	-	-
Dissosteira carolina	83, 84	multiplicated	89	-	90	91	99	103b, 103c	-	-	-
Schistocerca gregaria	85, 86	multiplicated	98i, ii	-	99	100	93	109i, ii	-	-	-
Stenobothrus lineatus	+ (2x)	multiplicated	+	-	+	+	+	+ (2 bdl)	-	-	-
Lentula callani	-	n.a.	89	-	90	91	99	103b, 103c	?	?	?
Lamarckiana sp.	1t.s.m., 2t.s.m. (in wingless female only strands)	multiplicated	?	?	1 t.r.c.	2 t.r.c.	d.e.m.	?	?	?	?
*Atractomorpha ambigua**	34, 35, 36	multiplicated	41	-	43	44	45	52, 53	-	-	-
Zonocerus elegans	83, 84	multiplicated			90	91	99				
Psednura sp.	?	?	?	?	?	?	+	?	-	?	?
Cephalocoema albrechti	-	n.a.	89	-	91	90	90a	103d	F	-	-
Different unindentified species: (P59) (P79) (P127)	-	n.a.	89 (P127)	-	90 (P127)	91 (P127)	99 (P127)	103c, 103b? (P127)	F (P127)	-	-
Xya sp.	-	n.a.	+	-	+	+	+	+	-	-	-
Timema nevadense	-	n.a.	-	+	+	+	+	+	+	+	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	lltpm2	lltpm3	lltpm4	lltpm5	lltpm6	lltpm7	lltpm8	lltpm9	lltpm10	lltpm11	lltpm12	lltpm13	llppm1
Papuaistus sp.	-	-	-	-	-	-	-	+ (?)	+	-	-	-	+
Hemideina crassidens	-	-	-	-	-	-	-	-	+	-	-	-	+
Stenopelmatus sp.	-	-	-	-	-	-	-	+ (?)	+	-	-	-	+
*Locusta migratoria manilensis**	45	-	-	46	-	-	-	47	48	-	-	-	-
Locusta migratoria	-	-	-	-	-	-	-	85	-	-	-	-	-
Dissosteira carolina	-	-	-	-	-	-	-	85	-	-	-	-	-
Schistocerca gregaria	90?	-	-	-	-	-	-	94	-	-	-	-	-
Stenobothrus lineatus	-	-	-	-	-	-	-	+	-	-	-	-	-
Lentula callani	?	?	?	?	?	?	?	-	?	?	?	?	?
Lamarckiana sp.	a.t.m.	?	?	?	?	?	?	p.a.m.	?	?	?	?	?
*Atractomorpha ambigua**	-	-	-	-	-	-	-	37, 38	-	-	-	-	-
Zonocerus elegans								85					
Psednura sp.	?	?	?	?	?	?	?	+	?	?	?	?	?
Cephalocoema albrechti	-	-	-	-	-	-	-	-	-	-	-	-	-
Different unindentified species: (P59) (P79) (P127)	-	-	-	-	-	-	-	tergopleural muscle (P127)	-	-	-	-	-
Xya sp.	-	-	-	-	-	-	-	+	-	-	-	-	-
Timema nevadense	-	-	-	-	-	-	-	-	-	-	-	+	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIppm2	IIspm1	IIspm2	IIspm3	IIspm4	IIspm5	IIspm6	IIspm7	IIspm8	IIspm9	IIpcm1	IIpcm2	IIpcm3
Papuaistus sp.	-	-	+	+	-	-	-	-	-	-	+	+	+
Hemideina crassidens	-	-	+	+	-	-	-	-	-	-	+	+	+
Stenopelmatus sp.	-	-	+	+	-	-	-	-	-	-	+	+	+
*Locusta migratoria manilensis**	-	49	50	69	-	-	-	-	-	-	-	61	59, 60
Locusta migratoria	-	97	86	-	-	-	-	-	-	-	-	98	94, 95
Dissosteira carolina	-	97	86	-	-	-	-	-	-	-	-	98	94, 95
Schistocerca gregaria	-	91	97	-	-	-	-	-	-	-	-	92	106, 107
Stenobothrus lineatus	-	+	+	-	-	-	-	-	-	-	-	+	+
Lentula callani	?	-	86	?	?	?	?	?	?	?	-	98	94, 95
Lamarckiana sp.	?	1p.e.m. (extremely reduced in wingless female)	?	?	?	?	?	?	?	?	?	2p.e.m.?	?
*Atractomorpha ambigua**	-	39	40	-	-	-	-	-	-	-	-	51	49, 50
Zonocerus elegans		97 (not present in micropterous forms)	86									98	
Psednura sp.	?	?	?	?	?	?	?	?	?	?	?	?	?
Cephalocoema albrechti	-	-	86	-	-	-	-	-	-	-	-	94	95
Different unindentified species: (P59) (P79) (P127)	-	-	86 (P127)	-	-	-	-	-	-	-	-	95	94 (P127)
Xya sp.	-	-	+	-	-	-	-	-	-	+	-	-	+
Timema nevadense	-	-	+	+	-	-	-	-	-	-	-	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIpcm4	IIpcm5	IIpcm6	IIvlm1	IIvlm2	IIvlm3	characteristics of IIvlm3	IIvlm4	IIvlm5	IIvlm6	IIvlm7	IIscm1	IIscm2	IIscm3
Papuaistus sp.	+	+	-	-	-	+	distinct muscle	-	+	-	-	+ (2x)	-	+
Hemideina crassidens	+	+	-	-	-	+	distinct muscle	-	+	-	-	+ (2x)	-	+
Stenopelmatus sp.	+	+	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
*Locusta migratoria manilensis**	60	-	-	-	-	67	sclerotized fiber	-	68	-	-	52	-	57
Locusta migratoria	96	-	-	-	-	116 (sclerotized fiber)	sclerotized fiber	-	117	-	-	92	-	100
Dissosteira carolina	96	-	-	-	-	116 (sclerotized fiber)	sclerotized fiber	-	117	-	-	92	-	100
Schistocerca gregaria	105	-	-	-	-	122 (sclerotized fiber)	sclerotized fiber	-	123	-	-	101	-	103
Stenobothrus lineatus	+	-	-	-	-	sclerotized fiber	sclerotized fiber	-	+	-	-	+	-	+
Lentula callani	96	?	?	?	?	?	?	?	117	?	?	?	?	100
Lamarckiana sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?
*Atractomorpha ambigua**	50	-	-	-	-	-	-	-	-	-	-	42	-	48
Zonocerus elegans														100
Psednura sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cephalocoema albrechti	96	-	-	-	-	-	-	-	117	-	-	92	-	100
Different unindentified species: (P59) (P79) (P127)	96 (P127)	-	-	-	-	-	-	-	117 (P127)	-	-	92 (P127)	-	100 (P127)
Xya sp.	+	-	-	-	-	+	distinct muscle	-	+	-	-	+	-	+
Timema nevadense	-	+	-	-	-	+	distinct muscle	-	-	-	-	+	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

	METATHORAX										
species	IIIscm4	IIIscm5	IIIscm6	IIIscm7	IIIdlm1	IIIdlm2	IIIdvm1	IIIdvm2	IIIdvm3	IIIdvm4	IIIdvm5
Papuaistus sp.	+	+	+	+	+	+	-	+	-	+	+
Hemideina crassidens	+	+	+	+	+	+	-	+	-	+	+
Stenopelmatus sp.	+	+	+	+	+	+	-	+	-	+	+
*Locusta migratoria manilensis**	56?	- (?)	63	81	66	-	71	80	-	84, 85	86
Locusta migratoria	101	93	103d	-	112	-	113	118	-	119	120
Dissosteira carolina	101	93	103d	-	112	-	113	118	-	119	120
Schistocerca gregaria	104	102	109iii	-	117	-	116	125	-	126	127
Stenobothrus lineatus	+	+	+	-	+	-	+	+	-	+	+
Lentula callani	101	93	103d	?	?	?	-	?	?	119	120
Lamarckiana sp.	?	?	?	?	d.l.m.	?	t.s.m.	?	?	1 t.r.c.	2 t.r.c.
*Atractomorpha ambigua**	47?	46	54	-	57, 58?	-	60	67	-	70	71
Zonocerus elegans	101	93			112		113	118			
Psednura sp.	?	?	?	?	?	?	?	?	?	?	?
Cephalocoema albrechti	101	93, 93a	103c	-	-	-	-	118	-	119a+b	119
Different unindentified species: (P59) (P79) (P127)	101 (P127)	93 (P127)	103d (P127)	-	-	-	-	118 (P127)	-	120 (P127)	119 (P127)
Xya sp.	+	-	+	-	?	-	-	+	-	+	?
Timema nevadense	-	-	-	+	+	+	-	-	+	+	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIIdvm6	IIIdvm7	IIIdvm8	IIItpm1	IIItpm2	IIItpm3	IIItpm4	IIItpm5	IIItpm6	IIItpm7	IIItpm8	IIItpm9
Papuaistus sp.	+	+	+	-	-	-	-	-	-	-	-	+ (?)
Hemideina crassidens	+	+	+	-	-	-	-	-	-	-	-	-
Stenopelmatus sp.	+	+	+	-	-	-	-	-	-	-	-	+ (?)
*Locusta migratoria manilensis**	87	95, 96	72	73	74	-	-	75	-	-	-	76
Locusta migratoria	129	133b, 133c	-	-	-	-	-	-	-	-	-	114a, b
Dissosteira carolina	129	133b, 133c	-	-	-	-	-	-	-	-	-	114
Schistocerca gregaria	120	137i, ii	-	-	-	-	-	-	-	-	-	121
Stenobothrus lineatus	+	+ (2 bdl)	-	-	-	-	-	-	-	-	-	+
Lentula callani	129	133b, 133c	140	?	?	?	?	?	?	?	?	-
Lamarckiana sp.	d.e.m.	?	?	?	a.t.m.	?	?	?	?	?	?	p.a.m.
*Atractomorpha ambigua**	72	79, 80	61	-	-	-	-	-	-	-	-	62, 63
Zonocerus elegans	129											114
Psednura sp.	+	?	+	?	?	?	?	?	?	?	?	+
Cephalocoema albrechti	120	133d	Fa	-	-	-	-	-	-	-	-	-
Different unindentified species: (P59) (P79) (P127)	129 (P127)	133b, 133c (P127)	Fa	-	tergopleural intersegmental muscle ? (P127)	-	-	-	-	-	-	tergopleural muscle (P127)
Xya sp.	+	-	+	-	-	-	-	-	-	-	-	+
Timema nevadense	+	+	+	-	-	-	-	-	-	-	-	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIItpm10	IIItpm11	IIItpm12	IIItpm13	IIIppm1	IIIppm2	IIIspm1	IIIspm2	IIIspm3	IIIspm4	IIIspm5	IIIpcm1	IIIpcm2	IIIpcm3	IIIpcm4
Papuaistus sp.	+	-	-	-	+	-	-	+	-	-	+	+	+	+	+
Hemideina crassidens	+	-	-	-	+	-	-	+	-	-	+	+	+	+	+
Stenopelmatus sp.	+	-	-	-	+	-	-	+	-	-	-	+	+	+	+
*Locusta migratoria manilensis**	-	-	-	-	-	-	77, 78	79	-	-	-	-	78	76	77
Locusta migratoria	-	-	-	-	-	-	127	115	-	-	-	-	128	125	126
Dissosteira carolina	-	-	-	-	-	-	127	115	-	-	-	-	128	125	126
Schistocerca gregaria	-	-	-	-	-	-	118, 119i	124	-	-	-	-	119ii	134	133
Stenobothrus lineatus	-	-	-	-	-	-	+	+	-	-	-	-	+	+	+
Lentula callani	?	?	?	?	?	?	-	115	?	?	?	-	128	125	126
Lamarckiana sp.	?	?	?	?	?	?	1 p.e.m. (extremely reduced in wingless female)	?	?	?	?	?	2p.e.m.?	?	?
*Atractomorpha ambigua**	-	-	-	-	-	-	64, 65	66	-	-	-	-	94	92	93
Zonocerus elegans							127 (not present in micropterous forms)	115					128	125	126
Psednura sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cephalocoema albrechti	-	-	-	-	-	-	-	115	-	-	-	-	125	125a	126
Different unindentified species: (P59) (P79) (P127)	-	-	-	-	-	-	-	115 (P127)	-	-	-	-	-	125 (P127)	126 (P127)
Xya sp.	-	-	-	-	-	-	-	+	-	-	-	-	-	+	+
Timema nevadense	-	-	-	+	-	-	-	+	-	-	-	+	+	+	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIIpcm5	IIIpcm6	IIIpcm7	IIIvlm1	IIIvlm2	IIIvlm3	IIIscm1	IIIscm2	IIIscm3	IIIscm4	IIIscm5	IIIscm6
Papuaistus sp.	+	-	-	-	+	+	+	+	+	+	-	+
Hemideina crassidens	+	-	-	-	+	+	+	+	+	+	-	+
Stenopelmatus sp.	+	-	-	-	+	+	+	+	+	+	-	+
*Locusta migratoria manilensis**	-	-	-	70	104?	103?	82, 83	88	90, 91	89	-	97
Locusta migratoria	-	-	-	-	144	143	121	123, 124	130	122	-	133d
Dissosteira carolina	-	-	-	-	+	+	121	123, 124	130	122	-	133d
Schistocerca gregaria	-	-	-	-	?	?	128	130, 131	132	129	-	137iii
Stenobothrus lineatus	-	-	-	-	+	+	+ (2x)	+ (2x)	+	+	-	+
Lentula callani	?	?	?	Transverse septal muscle	144	143	?	123	?	122	?	133d
Lamarckiana sp.	?	?	?	?	?	?	?	?	?	?	?	?
*Atractomorpha ambigua**	-	-	-	59	87?	86?	68, 69	73	75	74	-	81
Zonocerus elegans												
Psednura sp.	?	?	?	+	?	?	?	?	?	?	?	?
Cephalocoema albrechti	-	-	-	-	144?	143?	121, 121a	123, 124	130	130a	-	133c
Different unindentified species: (P59) (P79) (P127)	-	-	-	A, B (P127)	144 (P127)	143 (P127)	121 (P127) paired	123, 124 (P127)	130 (P127)	122 (P127)	-	133d (P127)
Xya sp.	-	-	-	+	+	+	+ (2x)	+ (2x)	+	+	-	+
Timema nevadense	+	-	-	-	+	-	+	+	+	-	-	+

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

			PROTHORAX							
taxon	**species**	**literature**	**Idlm1**	**Idlm2**	**Idlm3**	**Idlm4**	**Idlm5**	**Idlm6**	**Idvm1**	**Idvm2**
Phasmatodea	*Megacrania tsudai*	Maki 1935	65?	70	-	-	66, 68, 67?, 69?	67?, 69?	-	77
Mantophasmatodea	*Austrophasma caledonensis*	Wipfler *et al* 2015	m1	m2	m3	m2	m3	-	-	m4
Grylloblattodea	*Grylloblatta campodeiformis*	Walker 1938	45b	52, 45a	56?	51	56	-	-	46?
Blattodea	*Periplaneta americana*	Carbonell 1947	-	53	59	52	62	60, 61	57	58
Mantodea	*Stagmomantis carolina*	Levereault 1938	7a	7b	5	1c?	35	37	-	1a
Embioptera	*Embia ramburi*	Rähle 1970	M78	M68	M79	M69	M80, M81	-	-	M76
Embioptera	*Embia surcoufi* (male)	Barlet 1985a, b	?	?	?	?	?	?	?	?
Embioptera	*Embia surcoufi* (female)	Barlet 1985a, b	?	?	?	?	?	?	?	?
Dermaptera	*Euborellia annuliples*	Bharadwaj & Chadwick 19	1	2	8	-	-	-	v	7a
Zoraptera	*Zorotypus hubbardi* (winged morph)	Friedrich & Beutel 2008	Idlm1	Idlm2	Idlm3	Idlm4	Idlm5	-	Idvm1	Idvm2
Plecoptera	*Perla marginata*	Wittig 1955	Idlm10	0dlm1	Idlm11b	0dlm2	Idlm12	Idlm12?	0lm7	0lm7
Psocoptera	*Stenopsocus stigmaticus*	Badonnel 1934	Dpo	-	-	M. protergo-occ. obl.	Dpr	-	DVA	DVL_1
Thysanoptera	*Phloeothrips coreaceus*	Mickoleit 1961	M.lev.cap.prphr.	M.lev.cap.terg.	-	-	M.dors.obl.	-	M.compr.occ.	-
Neuroptera	*Palpares libelluides*	Czihak 1957	M.meson.occ.obl.	M.pron.occ.latus	Mm.meson.pron.	M.pron.occ.latus	Mm.meson.pron.	Mm.meson.pron.	-	M.cerv.occ.
Hymenoptera	*Macroxyela ferruginea*	Vilhelmsen 2000, Vilhelmsen *et al.* 2010	+	-	-	-	+	-	-	+
Archostemata (Coleoptera)	*Tetraphalerus bruchi*	Friedrich *et al.* 2009	M.2	M.2	M.3	-	M.6	-	-	M.15
Ephemeroptera	*Siphlonurus columbianus*	Matsuda 1956a	6	5	7, 8	4	10	9	-	2?

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ldvm3	ldvm4	ldvm5	ldvm6	characteristics of ldvm6	ldvm7	ldvm8	ldvm9	ldvm10	ldvm11	ldvm12	ldvm13	ldvm14
Megacrania tsudai	76	71	-	-	n.a.	-	-	-	101	102	-	81	81?
Austrophasma caledonensis	m5	m6	m7	m8	single	-	-	-	m9	-	-	m10	m11
Grylloblatta campodeiformis	46	-	48	47	single	-	-	-	58	-	-	60	-
Periplaneta americana	58?	54	64?	63, 64?, 69?	?	-	-	-	96	-	-	70	71, 72a+b, 73
Stagmomantis carolina	1b	6	2	3	single	-	-	-	36?	38	36?	9a?	9a?, b, c
Embia ramburi	M77	-	-	-	n.a.	-	-	-	M95, M96	-	-	M86	M87
Embia surcoufi (male)	?	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (female)	?	?	?	?	?	?	?	?	?	?	?	?	?
Euborellia annuliples	7b	-	5a, b	-	n.a.	-	-	-	14	-	-	16a	-
Zorotypus hubbardi (winged morph)	ldvm3	ldvm4	ldvm5	ldvm6	two bundles	-	-	-	ldvm10	-	-	ldvm13	ldvm14
Perla marginata	0lm8	0lm5	-	0lm6	single	-	-	-	lism22	lism24	-	ldvm15	ldvm16
Stenopsocus stigmaticus	DVL2 ?	T	-	S	single	-	-	-	U	-	-	-	-
Phloeothrips coreaceus	-	-	-	M.depr.cap.terg.	single	M.depr.cap.terg.?	-	-	M.prphr.-prfurc.	-	-	-	M.prom.cox.terg.troch.
Palpares libelluides	M.cerv.occ.	Mm.pron.occ.tenuis	M.pron.cerv.	-	n.a.	-	-	-	-	-	-	-	-.
Macroxyela ferruginea	+	-	-	+	single	?	?	+	+	-	-	-	-
Tetraphalerus bruchi	M.15	-	M.14	M.12	two bundles	-	-	M.11	M.16	-	-	M.22	-
Siphlonurus columbianus	2?	1	-	-	n.a.	-	-	-	-	-	40, 41	14?	14?

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ldvm15	ldvm16	ldvm17	ldvm18	ldvm19	characteristics of ldvm19	ltpm1	ltpm2	ltpm2-2	ltpm3	ltpm4
Megacrania tsudai	88	83	84	85	-	n.a.	-	-	-	74	75
Austrophasma caledonensis	m12	m13	m14	m15	m16	single	-	-	-	m17	m18
Grylloblatta campodeiformis	-	62	62	63	67a	single	-	-	-	54?	54
Periplaneta americana	74	81	78?, 79, 80	76, 77, 78?	85a+b	?	-	56	-	67, 68	65, 66
Stagmomantis carolina	19a	10a, b	13, 14	15, 16, 17	23c-e	three bundles; all originating at the posterior half of the protergum	-	-	-	20	21
Embia ramburi	M88	M92	M93, M91?	M89, M90, M91?	M94	single	-	-	-	M98	M99
Embia surcoufi (male)	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (female)	?	?	?	?	?	?	?	?	?	?	?
Euborellia annuliples	16b	18a	18b	18c	17	single	-	6	-	19	19
Zorotypus hubbardi (winged morph)	ldvm15	ldvm16	ldvm17	ldvm18	ldvm19	two anterior and one posterolateral bundle	ltpm1	ltpm2	-	ltpm3	ltpm4
Perla marginata	ldvm17?	ldvm19	ldvm20	ldvm21	ldvm18	single	-	0lm9	-	ltpm25	ltpm26
Stenopsocus stigmaticus	L	-	C	F	A	single	LL	DVL2 ?	-	G	G?
Phloeothrips coreaceus	M.prom.cox.terg.bascox.	M.rem.cox.terg.	M.rem.cox.terg.	M.rem.cox.terg.?	M.depr.troch.terg.	single	-	-	-	-	M.pl.-terg.
Palpares libelluides	M.pron.cerv.cox.	Mm.pron.cox.	Mm.pron.cox.	-	-	n.a.	-	-	-	Mm.pron.pl.div.?	Mm.pron.pl.div.
Macroxyela ferruginea	-	?	?	-	-	n.a.	-	-	-	+	+
Tetraphalerus bruchi	-	M.23	M.23	M.25	-	n.a.	-	-	-	M.17?	-
Siphlonurus columbianus	18	15	16	17	20	single	12?	11		13	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	ltpm5	ltpm6	ltpm7	lspm1	lspm2	origin of lspm2	lspm3	lspm4	lspm5	lspm6	lspm7	lpcm1	lpcm2	lpcm3	lpcm4	lpcm5
Megacrania tsudai	-	-	-	-	108	laterally on posterior margin of posterior sternal plate	-	-	78	-	-	-	-	82	89	-
Austrophasma caledonensis	-	m19?	-	m20	m21	posterior part of prospina	m28?	-	-	-	-	-	-	-	m22	-
Grylloblatta campodeiformis	54?	-	-	55	75	laterally on prospina	-	-	-	-	-	-	49	61?	-	-
Periplaneta americana	-	-	-	-	103	prospina	-	-	-	102	-	-	-	-	75	75?
Stagmomantis carolina	-	-	-	22	45	laterally on prospina	39?	-	-	-	-	4	-	-	19b	-
Embia ramburi	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	-	M100
Embia surcoufi (male)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (female)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Euborellia annuliples	-	-	-	-	-	n.a.	13	10	-	-	-	-	-	-	20b	-
Zorotypus hubbardi (winged morph)	ltpm5	-	-	lspm1	lspm2	lateral face of prospina	lspm3	-	-	-	-	-	-	-	lpcm4	lpcm5
Perla marginata	ltpm27?	-	-	lzm34	-	n.a.	-	-	-	-	-	-	-	-	-	lcpm28
Stenopsocus stigmaticus	-	-	-	-	h_2	lateral face of prospina	-	-	-	-	-	-	X_1	-	E	e
Phloeothrips coreaceus	-	-	-	M.furc-pl.	-	n.a.	-	-	-	-	-	M.cerv.-postocc.	-	-	-	M.abd.cox.pl.
Palpares libelluides	Mm.pron.pl.div.	-	-	-	-	n.a.	-	-	-	-	-	-	-	Mm.pleur.cox.?	Mm.pleur.cox.	Mm.pleur.cox.
Macroxyela ferruginea	-	-	-	-	-	n.a.	-	-	-	-	-	-	+	?	+	-
Tetraphalerus bruchi	-	M.18	-	-	-	n.a.	-	-	-	M.21x	-	-	-	-	M.24	-
Siphlonurus columbianus	-	-	-	-	-	n.a.	-	-	-	-	-	-	-	-	19	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	lpcm6	lpcm7	lpcm8	lvlm1	lvlm2	lvlm3	lvlm4	lvlm5	lvlm6	lvlm7	lvlm8	lvlm8 paired, unpaired	lvlm9
Megacrania tsudai	91	-	92	73	-	72	98	-	-	-	-	n.a.	-
Austrophasma caledonensis	-	-	m23	-	-	m24	m25		m26	m27	-	n.a.	-
Grylloblatta campodeiformis	-	-	67b	-	-	50	59	-	81	57	-	n.a.	80
Periplaneta americana	-	97	85c+d	84	-	55	99	-	101	100	106	?	104
Stagmomantis carolina	-	-	23b	-	-	8	-	-	-	-	42	paired	43, 44?
Embia ramburi	-	-	M101, M102	M71	-	M70	M84	M83	M85	M82	-	n.a.	-
Embia surcoufi (male)	?	?	?	?	?	?	?	+ (Fig.1; without description)	6	9	-	n.a.	5
Embia surcoufi (female)	?	?	?	?	?	?	?	+ (10) (Fig.1)	6	8	-	n.a.	9
Euborellia annuliples	20a	-	22a, b	4	5c	3	12	-	11	9	-	n.a.	-
Zorotypus hubbardi (winged morph)	-	-	lpcm8	-	-	lvlm3	lvlm4	-	lvlm6	lvlm7	-	n.a.	lvlm9
Perla marginata	-	-	lcpm29	0vlm4	-	0vlm3	lvlm14	-	-	lvlm13	-	n.a.	-
Stenopsocus stigmaticus	-	-	A`	-	LV_1	d_1, d_2	-	-	LVI_2	LVL_2	LVM_2	paired	-
Phloeothrips coreaceus	-	-	M.depr.troch.pl.	-	-	M.depr.cap.furc.lat.	M.prfurc.-prsp.	-	-	M.mesfurc.-profurc.	-	n.a.	M.mesfurc.-prsp.
Palpares libelluides	-	-	-	M.f.cerv.	-	Mm.f.tent.	-	-	-	M.furco-furc.	-	n.a.	-
Macroxyela ferruginea	+	-	?	+	-	+	+	-	-	+	-	n.a.	+
Tetraphalerus bruchi	-	-	M.31	M.10	-	M.9	-	-	-	M.42	-	n.a.	-
Siphlonurus columbianus	-	-	21?	3	-	26, 27	-	-	-	57	-	n.a.	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

								MESOTHORAX		
species	Ivlm10	Iscm1	Iscm2	Iscm3	Iscm4	Iscm5	Iscm6	Iscm7	IIdlm1	IIdlm2
Megacrania tsudai	-	86	87	90	-	-	-	-	-	93, 94, 95, 96
Austrophasma caledonensis	-	m29	m30	m31	m32, m33	-	m34	-	m35	m36
Grylloblatta campodeiformis	-	64	-	65	-	-	-	88	82	83
Periplaneta americana	-	-	-	83	82	98	-	105	110	111, 112, 113
Stagmomantis carolina	-	11	12	18	-	-	-	-	52?	52?, 53, 54
Embia ramburi	-	M103	M105	M104	-	-	-	-	?	?
Embia surcoufi (male)	-	?	?	?	?	?	?	8	1	2
Embia surcoufi (female)	-	?	?	?	?	?	?	11	1	2
Euborellia annuliples	-	21	-	-	-	-	23	43	24	25
Zorotypus hubbardi (winged morph)	-	?	Iscm2	Iscm3	-	-	-	Iscm7	IIdlm1	IIdlm2
Perla marginata	-	Ibm30	Ibm33	Ibm32	-	-	Ibm31	-	IIdlm35	IIdlm36, IIdlm37
Stenopsocus stigmaticus	-	m	-	Y	Y?	J	a	X_2	DL	DO
Phloeothrips coreaceus	-	-	-	M.add.cox.furc.	M.rem.cox.furc.	-	M.depr.troch.furc.	-	M.dors.rect.	-
Palpares libelluides	-	M.st.cox.	M.furcopleuro-cox.	-	M.furcopleuro-cox.?	M.mesost.procox.	M.abd.fem.f.	-	Mm.dors.r.	Mm.dors.obl.
Macroxyela ferruginea	-	+	+	-	+	+	+	-	?	?
Tetraphalerus bruchi	-	M.27	M.30	-	-	-	-	-	M.39	M.40
Siphlonurus columbianus	-	25	24	23	-	-	-	-	30	31

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIdvm1	characteristics of IIdvm1	IIdvm2	IIdvm3	IIdvm4	IIdvm5	IIdvm6	IIdvm7	IIdvm8	IIdvm9	IItpm1
Megacrania tsudai	-	n.a.	116?	116	117	118	127	130	100	103, 142	-
Austrophasma caledonensis	-	n.a.	m37	m38	m39	m40	m41	m42	-	-	m43
Grylloblatta campodeiformis	-	n.a.	86	-	87	-	-	98a	85	-	76
Periplaneta americana	121	single	118	119, 120	129, 130?	130?, 131	128	135a	125	-	108, 109
Stagmomantis carolina	48	single	62a	62b	65	65?	70	71c	55	-	47
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	17	single	32	32	33	-	34	35	18	-	25
Embia surcoufi (female)	-	n.a.	24	24	22?	-	23	25	17	-	28
Euborellia annuliples	-	n.a.	32	-	34a	34a?	34b	33	30	-	15
Zorotypus hubbardi (winged morph)	IIdvm1	multiplicated	IIdvm2	IIdvm3	IIdvm4	IIdvm5	IIdvm6	IIdvm7	IIdvm8	-	IItpm1
Perla marginata	Idvm40	single	IIdvm41	-	IIdvm43	IIdvm43	IIcpm53	IIdvm42	IIism44	-	IItpm46a
Stenopsocus stigmaticus	K	single	-	K`	I	C	F, F`	A	U	-	-
Phloeothrips coreaceus	M.st.-not.	pars cranialis/ pars dorsalis	-	-	-	M.rem.cox.terg.	M.rem.cox.terg.	-	M.mesphr.-mesfurc.	-	M.pl.-terg.epist.caud.
Palpares libelluides	M.scuto-st.	single	-	M.sc.trochantin.	Mm.sc.merales	Mm.sc.merales	M.subalar.mer.	M.abd.fem.sc.	-	-	Mm.n.epist.?
Macroxyela ferruginea	?	?	?	?	?	?	?	?	?	?	?
Tetraphalerus bruchi	M.44	single	-	-	M.60a	M.60b	M.64	M.69	M.45	-	-
Siphlonurus columbianus	43	single	32?	32?	33, 34	35	37	48	-	-	44

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IItpm2	IItpm3	IItpm4	IItpm5	IItpm6	IItpm7	IItpm8	IItpm9	IItpm10	IItpm11	IItpm12	IItpm13	IIppm1
Megacrania tsudai	-	-	-	105	115	-	-	114	106	-	-	104	107, 109
Austrophasma caledonensis	m44	m45	m46	m47	-	-	-	-	m48?	-	-	-	-
Grylloblatta campodeiformis	-	-	-	77	-	-	-	-	-	-	-	-	-
Periplaneta americana	-	-	116	-	114	-	-	115	-	-	-	-	-
Stagmomantis carolina	-	46	-	51	50	-	-	49	-	-	-	-	-
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	-	24	-	28?	-	26	-	27?	29	-	-	-	-
Embia surcoufi (female)	26?	27	-	32?	-	29?, 30	-	31?	33	-	-	-	-
Euborellia annuliples	-	-	37	37	38?	-	-	-	-	-	-	-	39?
Zorotypus hubbardi (winged morph)	-	-	IItpm4	-	IItpm6	IItpm7	-	IItpm9	IItpm10	-	-	-	-
Perla marginata	IItpm47	IItpm46b?	-	-	IItpm49	IItpm48	-	-	IIppm56	-	-	-	IIim65a
Stenopsocus stigmaticus	Z	V?	W_2, W_3	-	-	-	-	W_1	-	-	-	-	-
Phloeothrips coreaceus	M.pl.-terg.condyl.	-	-	-	-	M.pl.-pt.basalar.?	-	M.pl.-pt.?	-	M.pl.-terg.crist.pl	M.pl.-terg.epist.cran.?	-	-
Palpares libelluides	Mm.n.epist.?	Mm.n.epist.?	-	M.sc.pleurocost.l.	M.pleurocost.sc.	M.epis.al.	-	M.pleurocost.al.	M.epim.subal.	-	-	-	M.intraepist.
Macroxyela ferruginea	?	?	?	?	?	?	?	?	?	?	?	?	?
Tetraphalerus bruchi	M.47	-	-	-	M.46	M.53	-	M.54	-	-	-	-	-
Siphlonurus columbianus	42?	45	-	-	-	-	51	-	-	-	-	-	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIppm2	IIspm1	IIspm2	IIspm3	IIspm4	IIspm5	IIspm6	IIspm7	IIspm8	IIspm9	IIpcm1	IIpcm2	IIpcm3
Megacrania tsudai	-	110	111	148	-	-	-	-	-	-	122	123, 125, 126	129
Austrophasma caledonensis	-	m49	m50	m51	-	m52	-	-	-	-	-	-	m53
Grylloblatta campodeiformis	-	78	79	106	-	-	-	-	-	-	-	-	91
Periplaneta americana	-	-	117	149	-	-	-	-	-	-	122, 123, 124	-	126
Stagmomantis carolina	-	-	56	83	-	-	-	-	-	-	60	61, 63	64a, b
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	-	19, 21	23	51?	-	-	-	-	-	-	-	-	31
Embia surcoufi (female)	-	19?	21	46?	-	-	-	-	-	-	-	-	42
Euborellia annuliples	-	-	35, 40?	-	-	-	-	-	-	-	41	-	42
Zorotypus hubbardi (winged morph)	-	IIspm1	IIspm2	IIspm3	IIspm4	-	-	-	-	-	-	-	IIpcm3
Perla marginata	IIpm54a, IIpm54b	IIppm55	IIzm61a	-	-	-	-	-	-	-	-	IIcpm51	-
Stenopsocus stigmaticus	-	-	-	-	-	-	h_3	-	-	-	e	-	E
Phloeothrips coreaceus	M.pl.-terg.epist.cran.?	M.praecox.-basalar.	M.furc.-pl.	-	-	-	-	-	-	-	M.prom.cox.pl.troch.	-	-
Palpares libelluides	-	-	M.f.pleurocost.	-	-	-	M.metepist.mesof.	-	-	-	-	-	M.epist.cox.l.
Macroxyela ferruginea	?	?	?	?	?	?	+	?	?	?	?	?	?
Tetraphalerus bruchi	-	M.50	M.55	-	-	-	-	-	-	-	-	-	M.62
Siphlonurus columbianus	-	-	-	-	-	-	-	-	-	-	-	50	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIpcm4	IIpcm5	IIpcm6	IIvlm1	IIvlm2	IIvlm3	characteristics of IIvlm3	IIvlm4	IIvlm5	IIvlm6	IIvlm7	IIscm1	IIscm2	IIscm3
Megacrania tsudai	124	131	-	99	-	-	-	-	138, 139?	-	-	119, 120	121, 128?	128?
Austrophasma caledonensis	m54	m55	-	-	-	m56	distinct muscle	-	m57	-	-	m58	-	m59
Grylloblatta campodeiformis	-	98b	-	-	-	84	distinct muscle	-	111a	111b	-	89	-	93
Periplaneta americana	127	135c	-	-	-	148	distinct muscle	-	151, 152	189	-	133	132	-
Stagmomantis carolina	64c	71d	-	-	-	84	distinct muscle	-	-	-	-	66	68	-
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	30?	36	-	-	-	12	distinct muscle	-	10	-	-	43	40, 42	41
Embia surcoufi (female)	41?	40	-	-	-	10	distinct muscle	-	13	-	-	38	34, 37	35
Euborellia annuliples	-	47	-	29	-	26	distinct muscle	-	27	-	-	44	45	-
Zorotypus hubbardi (winged morph)	IIpcm4	IIpcm5	-	-	-	IIvlm3	distinct muscle	-	IIvlm5	-	-	IIscm1	IIscm2	IIscm3
Perla marginata	IIcpm52	IIcpm50	-	-	-	IIvlm38	distinct muscle	-	IIvlm39	-	-	IIbm57	IIbm60	IIbm59
Stenopsocus stigmaticus	e`	A`	-	-	-	LVL3	distinct muscle	-	LVl3	-	-	m	J	-
Phloeothrips coreaceus	M.abd.cox.pl.	-	-	-	-	M.mesfurc.-metfurc.	distinct muscle	-	-	-	M.mesfurc.-abdst.	M.prom.cox.furc.	M.rem.cox.furc.ventr.	-
Palpares libelluides	M.epist.cox.br.	-	M.abd.fem.epist.	-	-	M.furco-furcalis	distinct muscle	-	-	-	-	M.st.cox.ant.	M.st.cox.post.	-
Macroxyela ferruginea	?	?	?	?	?	+		?	+	?	?	?	?	?
Tetraphalerus bruchi	M.61	m.71	M.70	-	-	M.82	distinct muscle	-	M.83	-	-	M.65	M.67	-
Siphlonurus columbianus	36	47	-	59	-	-	n.a.	-	-	-	-	56	54	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

	METATHORAX										
species	IIscm4	IIscm5	IIscm6	IIscm7	IIIdlm1	IIIdlm2	IIIdvm1	IIIdvm2	IIIdvm3	IIIdvm4	IIIdvm5
Megacrania tsudai	-	-	-	-	-	133, 134, 135, 136	-	155?	155	156	157
Austrophasma caledonensis	m60	m62	m61	m63	m64	m65	-	m66	m67?	m67	m68
Grylloblatta campodeiformis	92	90	-	118	112	113	-	116	-	117	-
Periplaneta americana	-	134	135b	173	153	154, 155, 156	-	161, 162	163	175?, 176	174, 175?
Stagmomantis carolina	69	67	71b	-	89?	89?, 90	-	95	95?	97	97?
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	39	38?	37	11	3	4	45	63?	63	64	-
Embia surcoufi (female)	36	12?	39	14	4	5	-	50?	52	48?	-
Euborellia annuliples	46	-	48	65	49, 54?	50a, b	-	-	55	57a	-
Zorotypus hubbardi (winged morph)	IIscm4	-	IIscm6	IIscm7	IIIdlm1	IIIdlm2	IIIdvm1	IIIdvm2	IIIdvm3	IIIdvm4	IIIdvm5
Perla marginata	IIzm61b	-	IIbm58	-	IIIdlm35	IIIdlm36, IIIdlm37	IIIdvm40	IIIdvm41	-	IIIdvm43	IIIdvm43
Stenopsocus stigmaticus	Y	-	a	X_3	DL	DO	K	-	-	I	C
Phloeothrips coreaceus	M.rem.cox.furc.dors.	M.rem.cox.furc.ventr.?	M.depr.troch.furc.	M.mesfurc.metcox.	M.dors.rect.	M.metnot.abdterg., Mdors.obl.	M.st.-not.	-	-	-	M.rem.cox.terg.
Palpares libelluides	-	-	M.abd.fem.f.	-	Mm.dors.r.	Mm.dors.obl.	Mm.scuto.-st.	-	M.sc.trochantin.	Mm.sc.mer.	Mm.sc.mer.
Macroxyela ferruginea	?	?	?	?	+	+	+	+	-	+	+
Tetraphalerus bruchi	M.66	-	M.72	-	M.79	M.80	M.84	-	-	M.101	M.102
Siphlonurus columbianus	55	-	-	-	63	64	71	65?	65?	66	67

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIIdvm6	IIIdvm7	IIIdvm8	IIItpm1	IIItpm2	IIItpm3	IIItpm4	IIItpm5	IIItpm6	IIItpm7	IIItpm8	IIItpm9
Megacrania tsudai	165	167	141	143?	-	144, 143?	145	146	154	-	-	153
Austrophasma caledonensis	m69	m70	-	m71	m72	m73	m74	m75	-	-	-	-
Grylloblatta campodeiformis	-	128a	115	107	-	-	-	108	-	-	-	-
Periplaneta americana	169	177a	190	150	-	-	159	-	157	-	-	158
Stagmomantis carolina	102	103c	91	85	-	-	-	88	87	-	-	86
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	65	66	46	54	-	53	-	57?	-	55	-	56?
Embia surcoufi (female)	49	51	47?	54	52?	53	-	58?	-	55?, 56	-	57?
Euborellia annuliples	57b	56	53	31	36, 60?	-	36?	59?	61	-	-	-
Zorotypus hubbardi (winged morph)	IIIdvm6	IIIdvm7	IIIdvm8	IIItpm1	-	-	IIItpm4	-	IIItpm6	IIItpm7	-	IIItpm9
Perla marginata	IIIcpm53	IIIdvm42	IIIism44	IIItpm46a	IIItpm47	IIItpm47b	-	-	IIItpm49	IIItpm48	-	-
Stenopsocus stigmaticus	F, F`	A	U	p	Z	V?	W_2, W_3	-	-	-	-	W_1
Phloeothrips coreaceus	M.cox.-subalar.	M.depr.troch.terg.	M.metfurc.-metphr.	-	M.pl.-terg.condyl.	-	M.pl.-terg.crist.pl.	M.pl.-terg.crist.pl.	-	-	-	Mpl.-pt.?
Palpares libelluides	M.subal.mer.	M.abd.fem.sc.	M.metepist.mesofurc.?	Mm.n.epist.?	Mm.n.epist.?	Mm.n.epist.?	-	M.sc.pleurocost.l.	M.pleurocost.sc.	-	-	M.pleurocost.al.
Macroxyela ferruginea	+	?	+	+	+	+	-	+	-	+	-	+
Tetraphalerus bruchi	M.105	M.111	M.85, M.86	M.89	M.90	M.93	-	-	-	M.96	-	M.95
Siphlonurus columbianus	69	74	-	72	-	73	-	-	-	-	76	-

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIItpm10	IIItpm11	IIItpm12	IIItpm13	IIIppm1	IIIppm2	IIIspm1	IIIspm2	IIIspm3	IIIspm4	IIIspm5	IIIpcm1	IIIpcm2	IIIpcm3	IIIpcm4
Megacrania tsudai	147 (partial)	-	-	147 (partial)	151	-	149, 150?	152	-	-	-	-	160, 162, 163	166	161
Austrophasma caledonensis	m76?	-	-	-	-	-	m77	m78	-	-	m79	-	-	m80	m81
Grylloblatta campodeiformis	-	-	-	-	-	-	109	110	-	-	-	-	-	121	-
Periplaneta americana	-	-	-	-	-	-	-	160	-	-	-	164?, 165?, 166?	164, 165, 166	167	168
Stagmomantis carolina	-	-	-	-	-	-	-	92	-	-	-	93	94	96a, b	96c
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	58	-	-	-	-	-	48, 50	52	-	-	-	-	-	62	61
Embia surcoufi (female)	59	-	-	-	-	-	45?	47	-	-	-	-	-	68	67?
Euborellia annuliples	-	-	-	-	62?	-	-	58	-	28	-	63a, b	-	-	64
Zorotypus hubbardi (winged morph)	IIItpm10	-	-	-	-	-	IIIspm1	IIIspm2	-	-	-	-	-	IIIpcm3	IIIcpm4
Perla marginata	IIIppm56	-	-	-	IIIim65a	IIIppm54a, IIIppm54b	IIIppm55	IIIzm61	-	-	-	-	IIIcpm51	-	IIIcpm52
Stenopsocus stigmaticus	-	-	-	-	-	-	-	-	-	-	-	e	-	E	e`
Phloeothrips coreaceus	-	-	-	-	-	M.pl.-basalar.	M.praecox.-basalar.	M.furc.-pl.	-	-	-	-	-	-	M.abd.cox.pl.
Palpares libelluides	M.epim.subal.	-	-	-	M.intraepist	-	-	M.f.pleurocost.	-	-	-	-	-	M.epist.cox.l.	M.epist.cox.br.
Macroxyela ferruginea	+	-	-	-	?	-	+	+	-	-	-	-	?	?	+
Tetraphalerus bruchi	-	-	-	-	M.97	-	M.98	-	-	-	-	-	-	M.104	M.103
Siphlonurus columbianus	-	-	-	-	-	-	-	+	-	-	-	-	78	-	68

Supplementary Table 1. Proposed homology of thoracic muscles based on the nomenclature of Friedrich & Beutel (2008) with the studies of different authors. Characters in yellow represent novel characteristics that are included in the cladistic analysis. Colour code for species/literature: blue - incomplete description of thoracic musculature; orange - complete description of thoracic musculature, no data on the skeletal morphology (thereof species not included in cladistic analysis); green - first description of thoracic musculature by author of the present study. *(continued)*

species	IIIpcm5	IIIpcm6	IIIpcm7	IIIvlm1	IIIvlm2	IIIvlm3	IIIscm1	IIIscm2	IIIscm3	IIIscm4	IIIscm5	IIIscm6
Megacrania tsudai	-	-	-	140	-	-	158	159, 165?	165?	-	-	168
Austrophasma caledonensis	m82	-	-	-	m83	-	m84	-	m85	m86	m87	m88
Grylloblatta campodeiformis	128b	-	-	-	114	-	119	-	123	122	120	-
Periplaneta americana	177c	-	-	191?, 192?	191?, 192?, 193	-	-	172	171?	170, 171?	-	177b
Stagmomantis carolina	103d	-	-	-	abd9	abd10	98	99	101	100	-	103b
Embia ramburi	?	?	?	?	?	?	?	?	?	?	?	?
Embia surcoufi (male)	67	-	-	-	13, 14	-	73	69, 72	71	70	-	68
Embia surcoufi (female)	66	-	-	-	15, 16	-	64	60, 63	61	62	-	65
Euborellia annuliples	69	-	-	-	51, 52a, b	-	66	67	66	68	-	70
Zorotypus hubbardi (winged morph)	IIIpcm5	-	-	-	IIIvlm2	-	IIIscm1	IIIscm2	IIIscm3	IIIscm4	-	IIIscm6
Perla marginata	IIIcpm50	-	-	-	IIIvlm64	-	IIIbm57	IIIbm60	IIIbm59	-	-	IIIbm58
Stenopsocus stigmaticus	A`	-	H	-	lv	-	m	J	-	-	-	a
Phloeothrips coreaceus	M.depr.troch.pl.	-	-	-	M.metfurc.-abdst.	-	M.prom.cox.furc.	M.rem.cox.furc.ventr.	-	M.rem.cox.furc.dors.	-	M.depr.troch.furc.
Palpares libelluides	-	M.abd.fem.epist.	-	-	-	-	M.st.cox.ant.	M.st.cox.post.	-	-	-	-
Macroxyela ferruginea	-	-	-	-	+	-	+	+	-	+	-	+
Tetraphalerus bruchi	-	-	-	-	fam	-	M.107	M.109	-	M.108	-	M.113
Siphlonurus columbianus	75	-	-	81	80	-	+	+	?	+	?	-

Supplementary Table 2. Character matrix used in cladistic analysis. Complete dataset includes characters of the thoracic skeleton (yellow), thoracic musculature (green) + wing and wing base (blue). Reduced dataset excludes characters of the wing and wing base (blue). "?" character state or homologization unsure; *"-"* inapplicable data.

| | | characters of the thoracic skeleton | | |

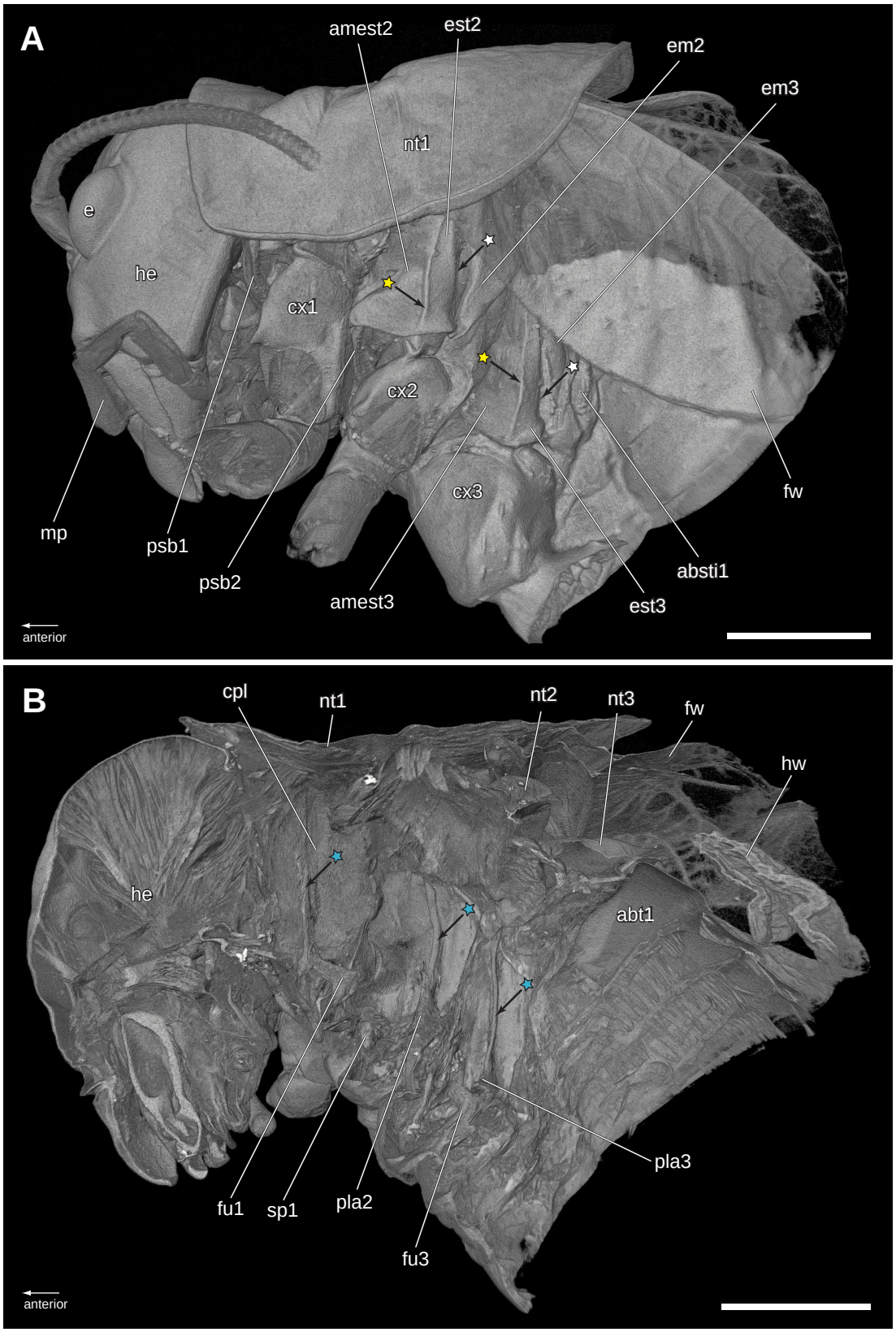
Supplementary Table 2. Character matrix used in cladistic analysis. Complete dataset includes characters of the thoracic skeleton (yellow), thoracic musculature (green) + wing and wing base (blue). Reduced dataset excludes characters of the wing and wing base (blue). "?" character state or homologization unsure; *"-"* inapplicable data. *(continued)*

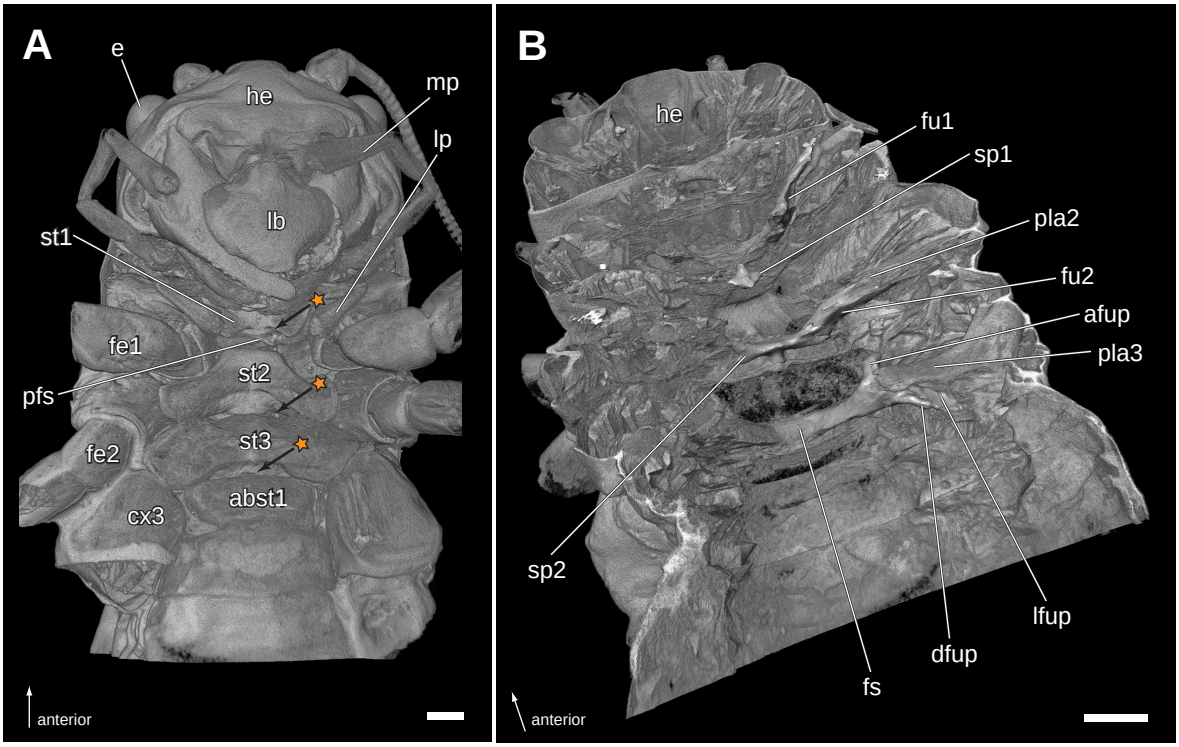
| | characters of the thoracic musculature | | |

Supplementary Table 2. Character matrix used in cladistic analysis. Complete dataset includes characters of the thoracic skeleton (yellow), thoracic musculature (green) + wing and wing base (blue). Reduced dataset excludes characters of the wing and wing base (blue). "?" character state or homologization unsure; *"-"* inapplicable data. *(continued)*

| | characters of the wing and wing base | | |

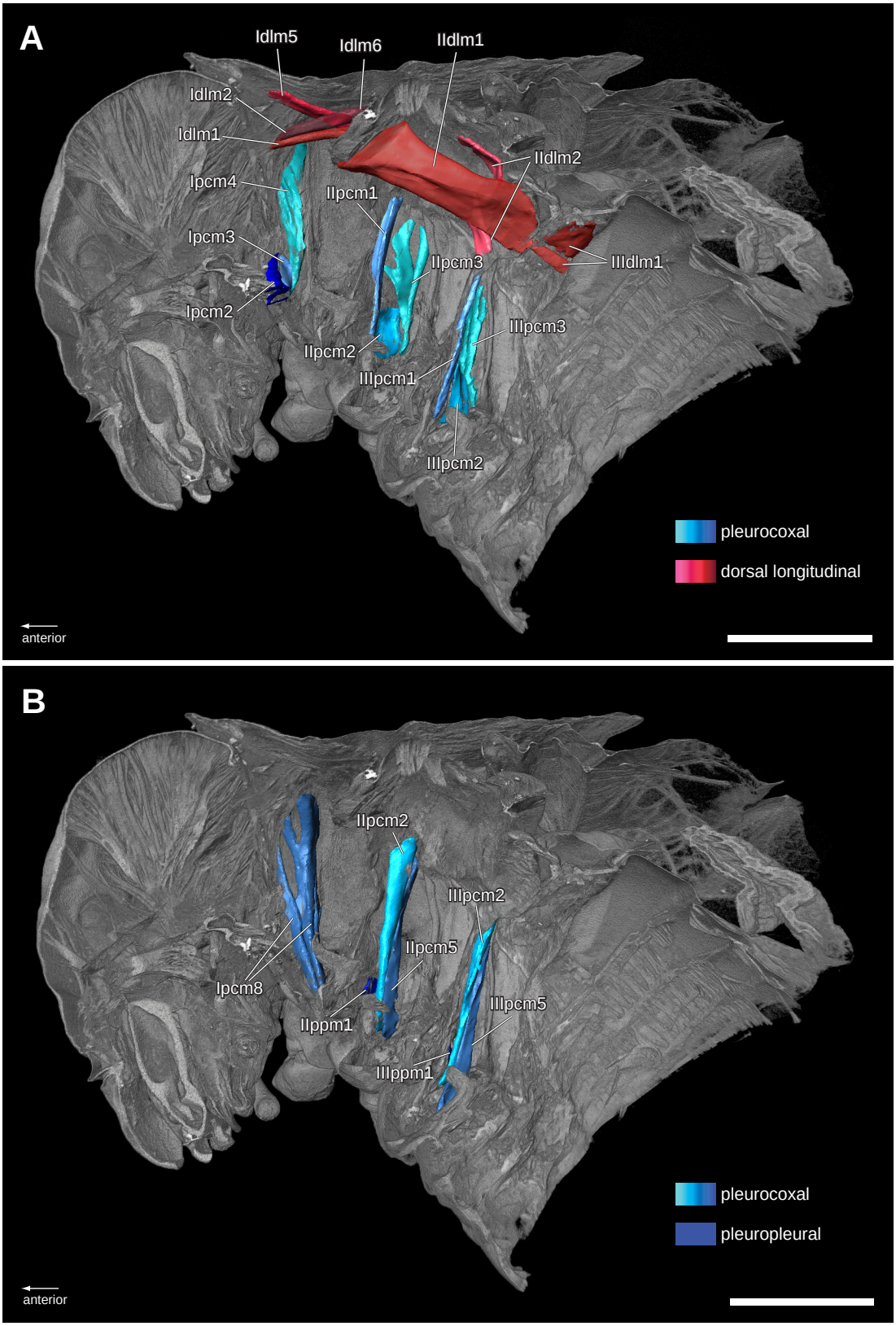
Supplementary Plate 1 (see opposite page). Thoracic skeleton of *Cyphoderris* sp. (Ensifera: Prophalangopsidae). Male. Three-dimensional reconstruction based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Yellow asterisks mark the strongly sclerotized edge between episternum and its anterior margin. Blue asterisks mark pleural ridge. Abbreviations: *absti* first abdominal stigma, *abt* first abdominal tergum, *amest2/3* anterior margin of mes-/metepisternum, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *em2/3* mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *fw* forewing, *he* head, *hw* hindwing, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm, *psb1/2* pro-/mesothoracic pleurosternal bridge, *sp1/2* pro-/mesospina. Scale bars: 5mm.


A
amest2
est2
em2
em3
nt1
e
he
cx1
cx2
cx3
mp
psb1
psb2
amest3
est3
absti1
fw
anterior
B
cpl
nt1
nt2
nt3
fw
hw
he
abt1
pla3
fu1
sp1
pla2
fu3
anterior

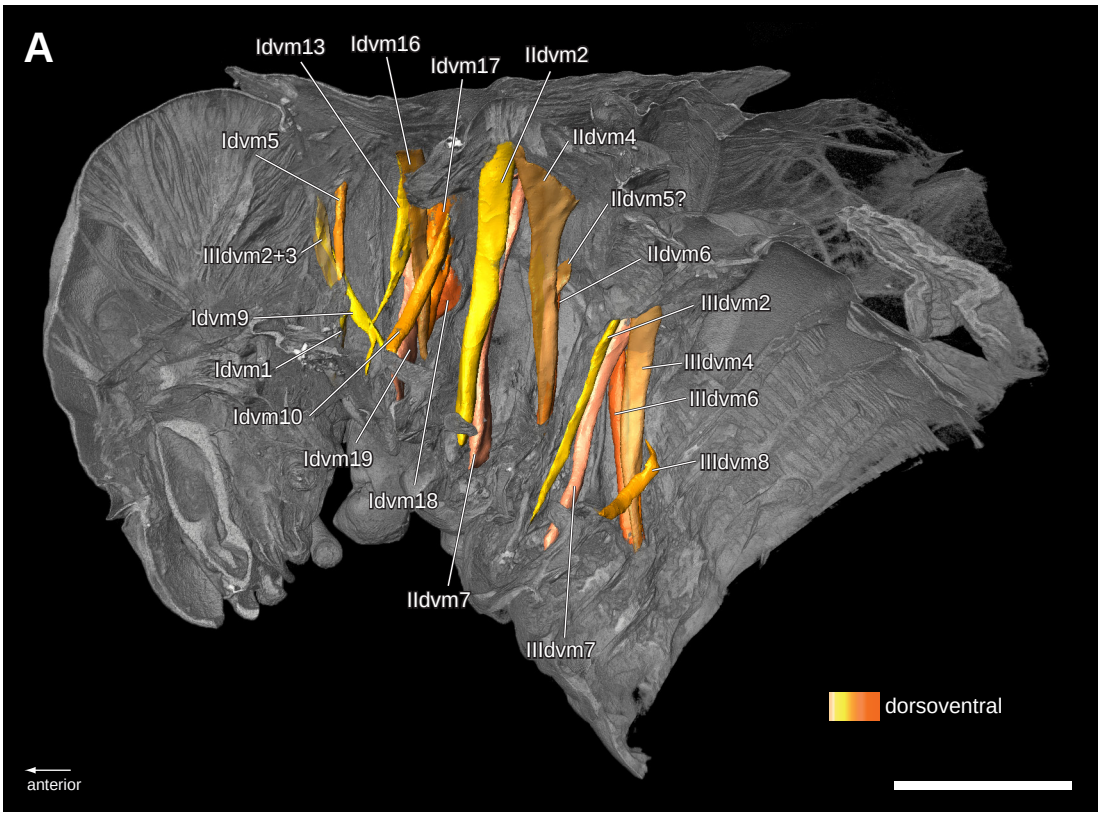


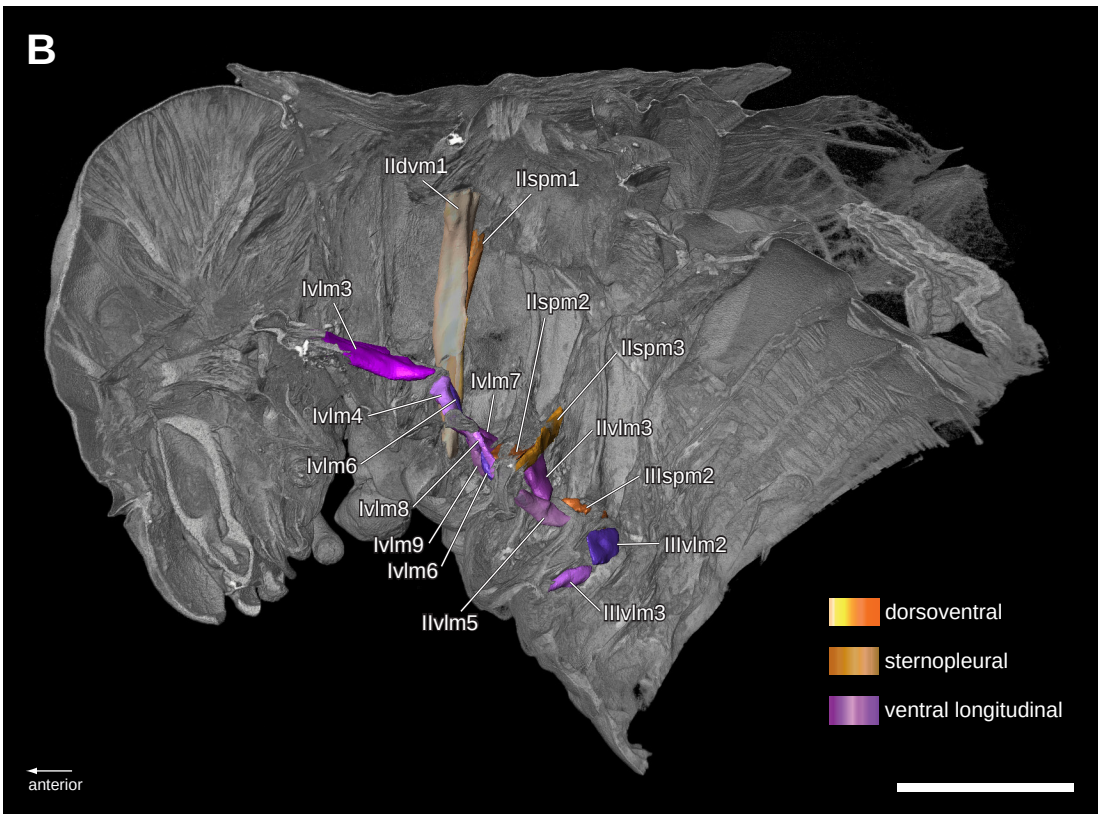
Supplementary Plate 2. Thoracic skeleton of *Cyphoderris* sp. (Ensifera: Prophalangopsidae). Male. Three-dimensional reconstruction based on µCT-sections. (A) Exterior ventral view. Orange asterisks mark furcal pits of pro-, meso- and metafurca. (B) Slightly shifted interior ventral view. Dorsal body half clipped off. Sternal apophyses (furcae and spinae) rendered in grey. Abbreviations: *abst* first abdominl sternum, *afup* anterior furcal process, *cx1/2/3* pro-/meso-/metacoxa, *dfup* dorsal furcal process, *e* compound eye, *fe1/2* pro-/mesothoracic femur, *fs* furcal stem, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lfup* lateral furcal process, *lb* labrum, *lp* labial palp, *nt1/2/3* pro-/meso-/metanotum, *pfs* postfurcasternite, *pla2/3* meso-/metathoracic pleural arm, *psb1/2* pro-/mesothoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *st1/2/3* pro-/meso-/metasternum. Scale bars: 1mm.

Supplementary Plate 3 (see opposite page). Thoracic musculature of *Cyphoderris* sp. (Ensifera: Prophalangopsidae). Male. Three-dimensional reconstruction based on µCT-sections. Right body half. Interior lateral view. (A) Dorsal longitudinal muscles (dlm) and pleurocoxal muscles (pcm). II/IIIpcm4 not illustrated. (B) Pleuropleural musles (ppm) and pleurocoxal muscles (pcm). Virtual dissection of pcm. Meso- and metathracic pcm2 is divided in a short (A) and a long (B) bundle. Scale bars: 5mm.

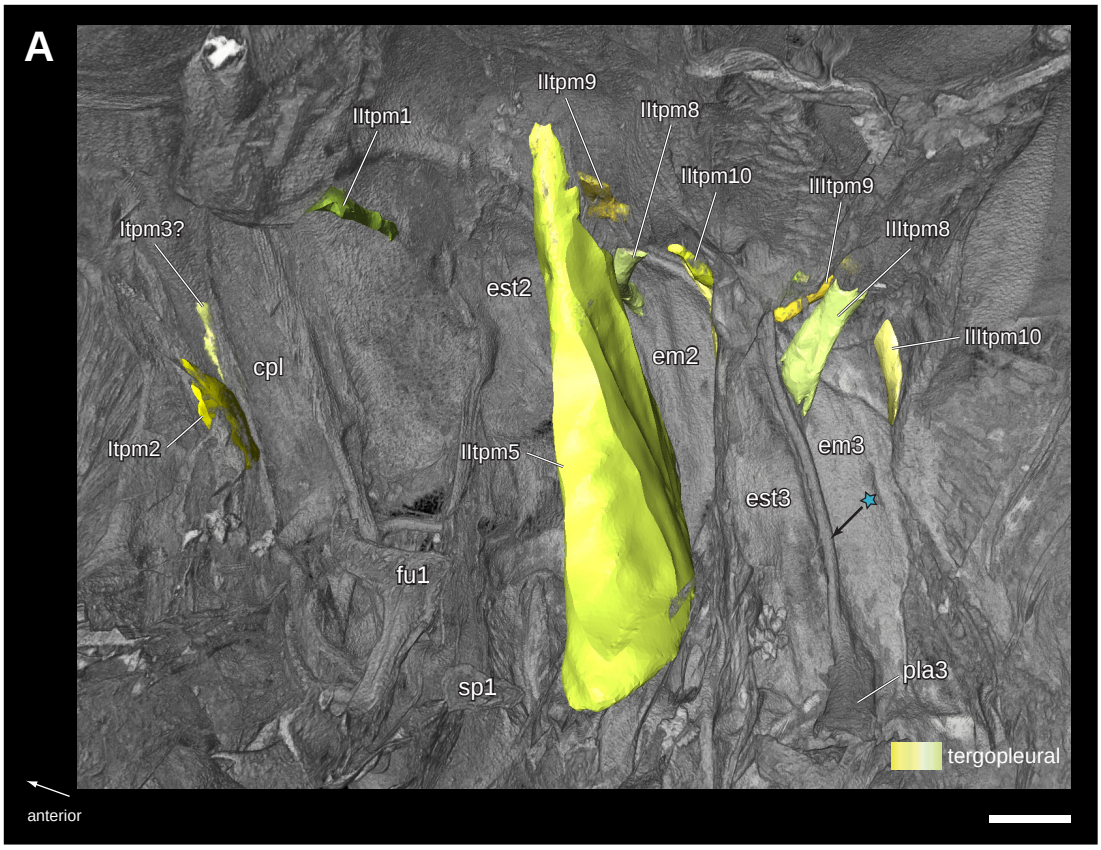

A
Idlm5
Idlm6
IIdlm1
Idlm2
Idlm1
IIdlm2
Ipcm4
IIpcm1
Ipcm3
IIpcm3
IIIdlm1
Ipcm2
IIIpcm3
IIpcm2
IIIpcm1
IIIpcm2
pleurocoxal
dorsal longitudinal
anterior
B
IIpcm2
IIIpcm2
IIpcm5
Ipcm8
IIIpcm5
IIppm1
IIIppm1
pleurocoxal
pleuropleural
anterior

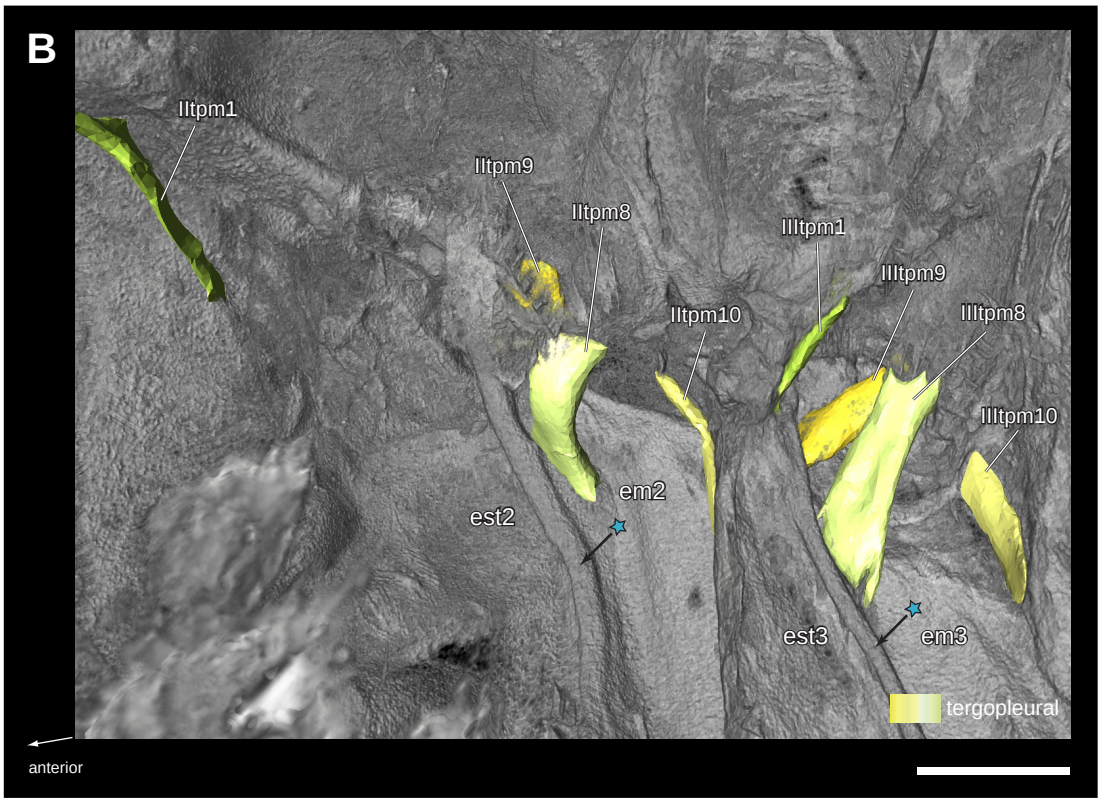
Supplementary Plate 4 (see opposite page). Thoracic musculature of *Cyphoderris* (Ensifera: Prophalangopsidae). Male. Three-dimensional reconstruction based on µCT-sections. Right body half. Interior lateral view. (A) Dorsalventral muscles (dvm). (B) IIdvm1, sternopleural muscles (spm) and ventral longitudinal muscles (vlm). Scale bars: 5mm.


A
Idvm13
Idvm16
Idvm17
IIdvm2
Idvm5
IIdvm4
IIdvm5?
IIIdvm2+3
IIdvm6
IIIdvm2
Idvm9
Idvm1
IIIdvm4
IIIdvm6
Idvm10
Idvm19
IIIdvm8
Idvm18
IIdvm7
IIIdvm7
dorsoventral
anterior

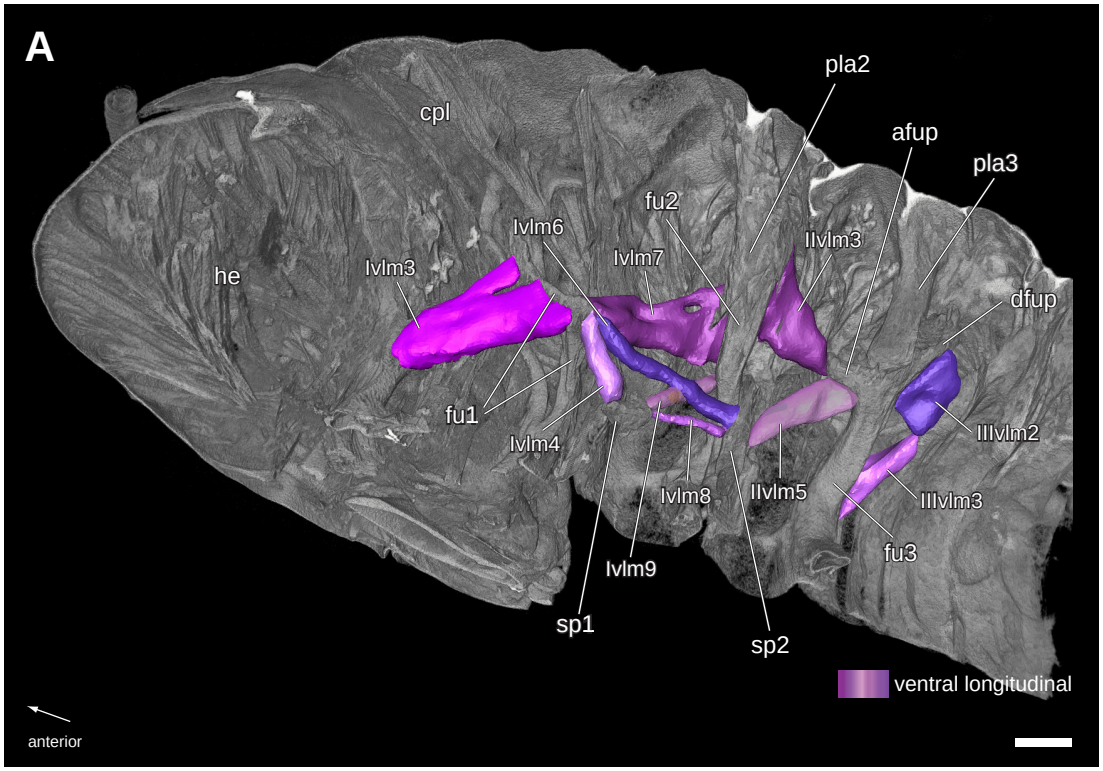

B
IIdvm1
IIspm1
Ivlm3
IIspm2
IIspm3
Ivlm7
Ivlm4
IIvlm3
Ivlm6
IIIspm2
Ivlm8
Ivlm9
IIIvlm2
Ivlm6
IIvlm5
IIIvlm3
dorsoventral
sternopleural
ventral longitudinal
anterior

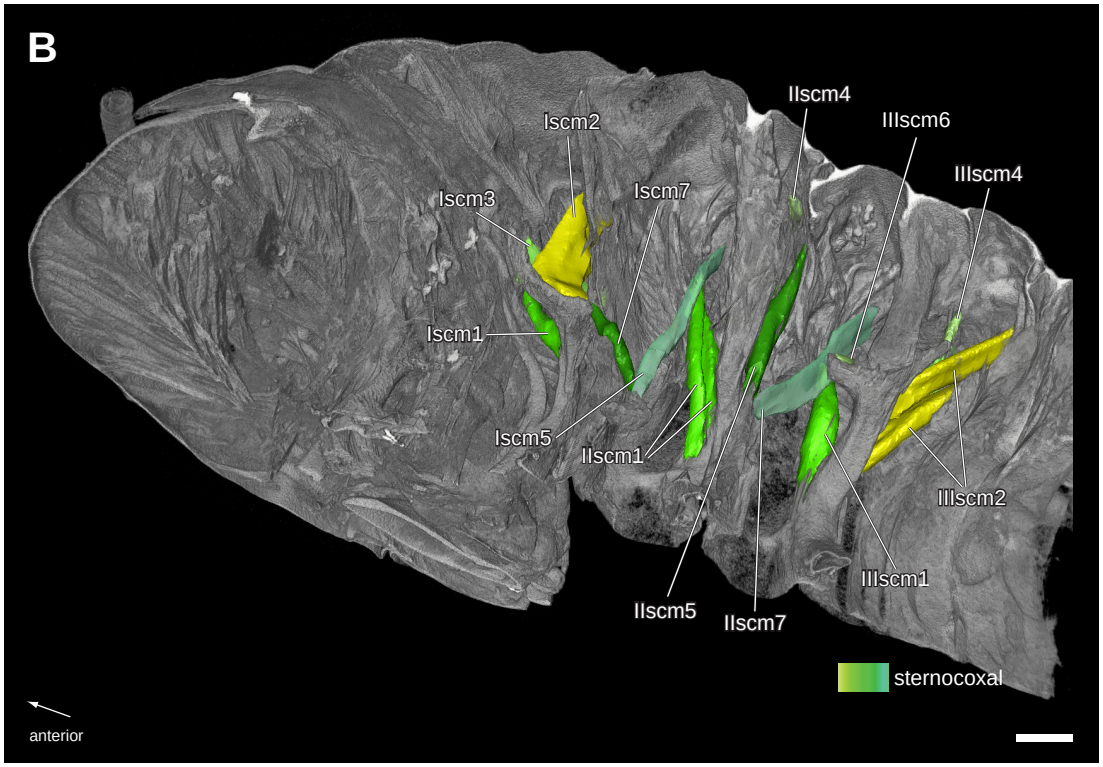
Supplementary Plate 5 (see opposite page). Thoracic musculature of *Cyphoderris* sp. (Ensifera: Prophalangopsidae). Male. Three-dimensional reconstruction based on µCT-sections. Right body half. Interior lateral view. Blue asterisks mark pleural ridge. Tergopleural muscles (tpm). (A) Pro-, meso- and metathoracic tergopleural muscles. (B) Pterothoracic tpm in slightly rotated lateral view. Abbreviations: *cpl* cryptopleura, *em2/3* mes-/metepimeron, *est2/3* mes-/metepisternum, *fu1* profurca, *pla3* metathoracic pleural arm, *sp1* prospina. Scale bars: 5mm.


A
lltpm1
lltpm9
lltpm8
lltpm10
lltpm3?
est2
lllltpm9
lllltpm8
lllltpm10
em2
cpl
ltpm2
lltpm5
em3
est3
fu1
sp1
pla3
tergopleural
anterior

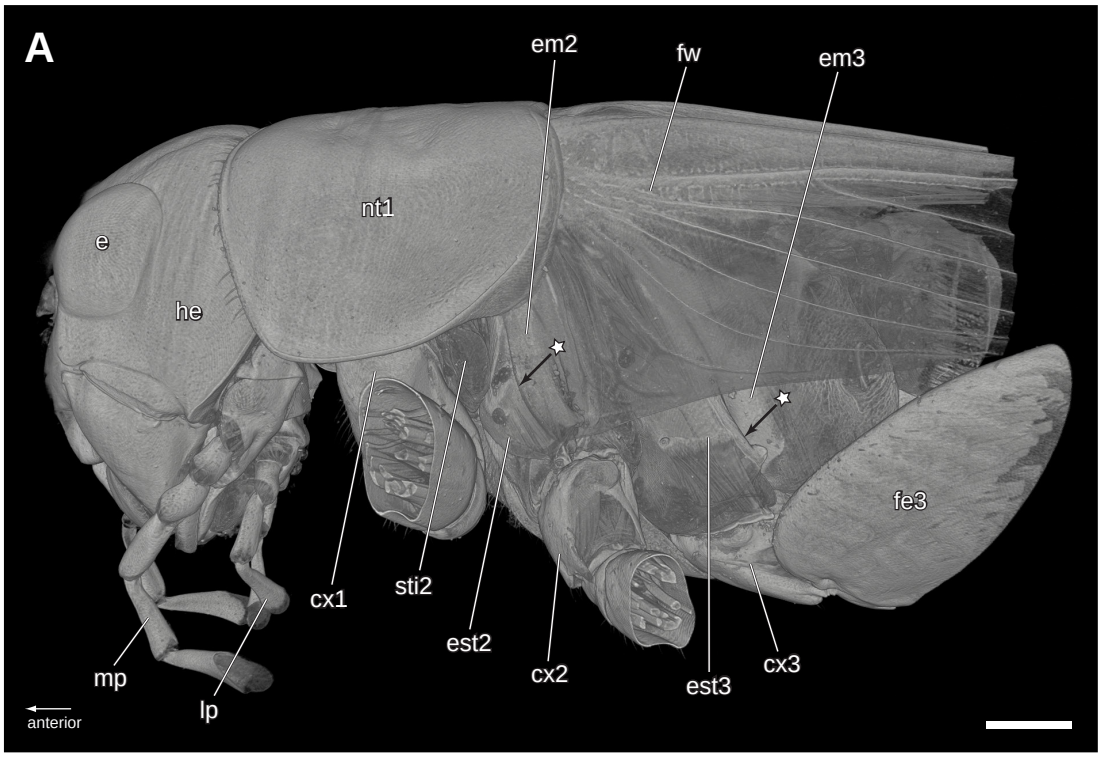

B
lltpm1
lltpm9
lltpm8
lllltpm1
lllltpm9
lltpm10
lllltpm8
lllltpm10
em2
est2
est3
em3
tergopleural
anterior

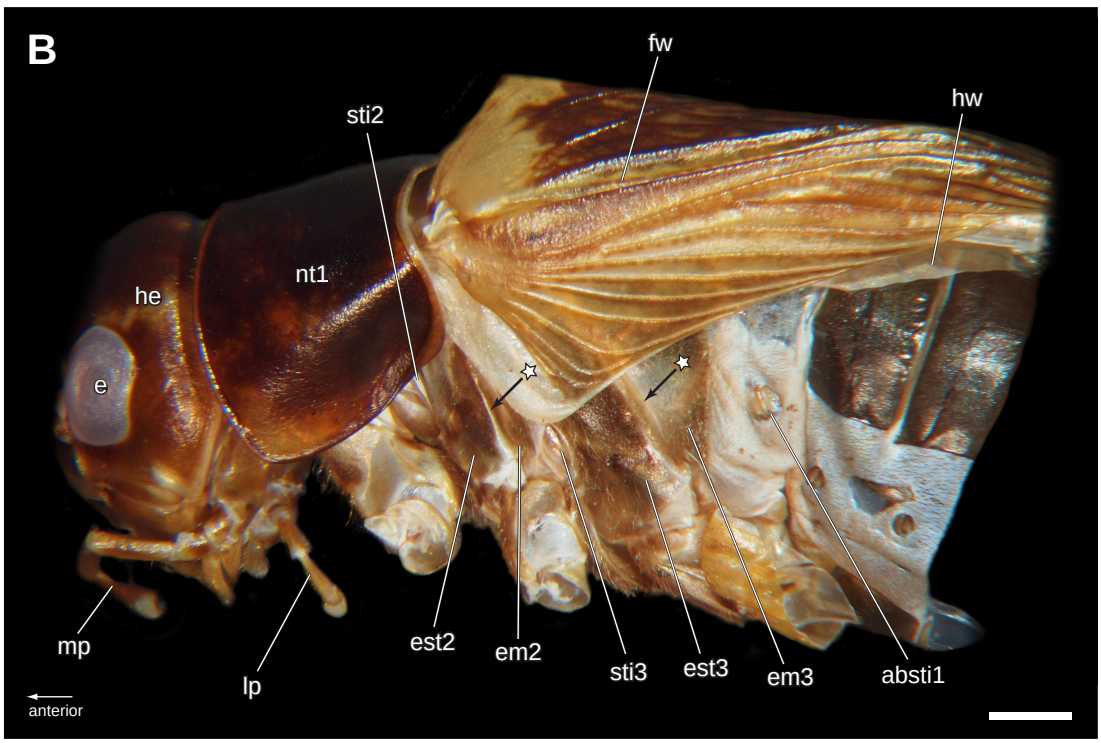
Supplementary Plate 6 (see opposite page). Thoracic musculature of *Cyphoderris* sp. (Ensifera: Prophalangopsidae). Male. Three-dimensional reconstruction based on µCT-sections. Upper body half clipped off. Interior ventral view. (A) Ventral longitudinal muscles (vlm). (B) Sternocoxal muscles (scm). Abbreviations: *afup* anterior furcal process, *cpl* cryptopleura, *dfup* dorsal furcal process, *fu1/2/3* pro-/meso-/metafurca, *he* head, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.


A
pla2
cpl
afup
pla3
fu2
lvlm6
IIvlm3
lvlm7
lvlm3
he
dfup
fu1
IIIvlm2
lvlm4
lvlm8
IIvlm5
IIIvlm3
fu3
lvlm9
sp1
sp2
ventral longitudinal
anterior

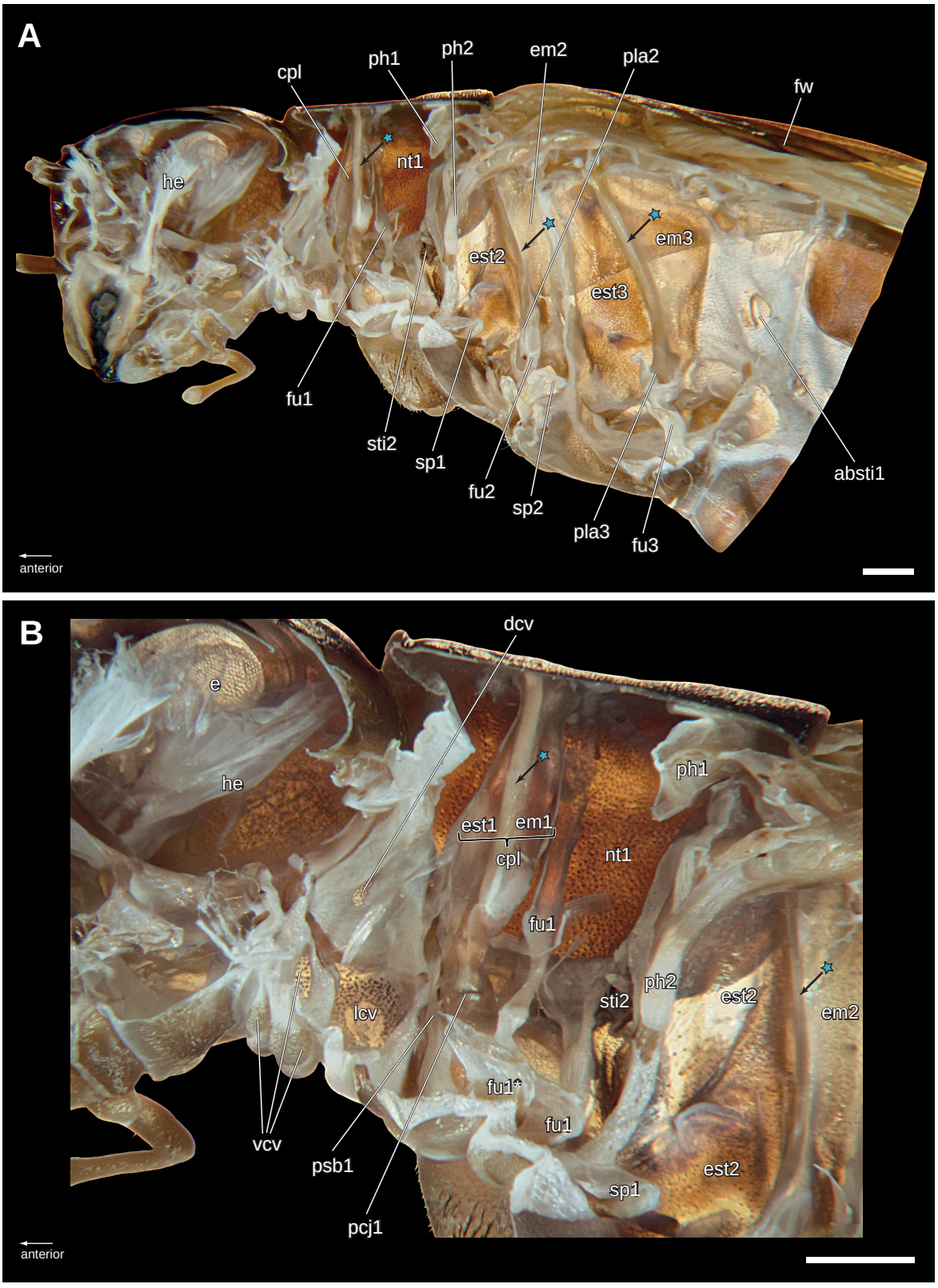

B
IIscm4
Iscm2
IIIscm6
IIIscm4
Iscm3
Iscm7
Iscm1
Iscm5
IIscm1
IIIscm2
IIIscm1
IIscm5
IIscm7
sternocoxal
anterior

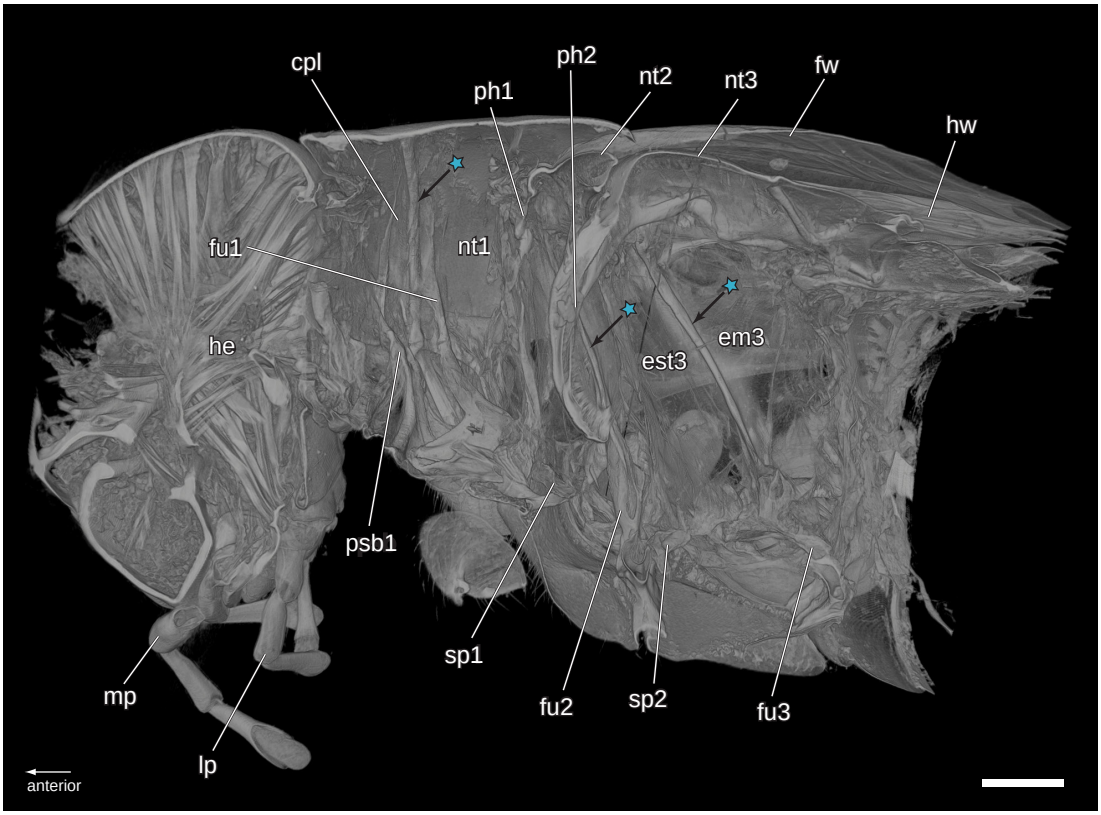
Supplementary Plate 7 (see opposite page). Thoracic skeleton of *Gryllus bimaculatus* (Ensifera: Gryllidae). Female. Exterior lateral view. Legs removed. **(A)** Three-dimensional reconstruction based on µCT-sections. (B) Phtograph. White asterisks mark pleural suture. Abbreviations: *absti* first abdominal stigma, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *em2/3* mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fe3* metafemur, *fw* forewing, *he* head, *hw* hindwing, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *sti2/3* meso-/metathoracic stigma. Scale bars: 1mm.


A
em2
fw
em3
nt1
e
he
fe3
cx1
sti2
est2
cx2
est3
cx3
mp
lp
anterior

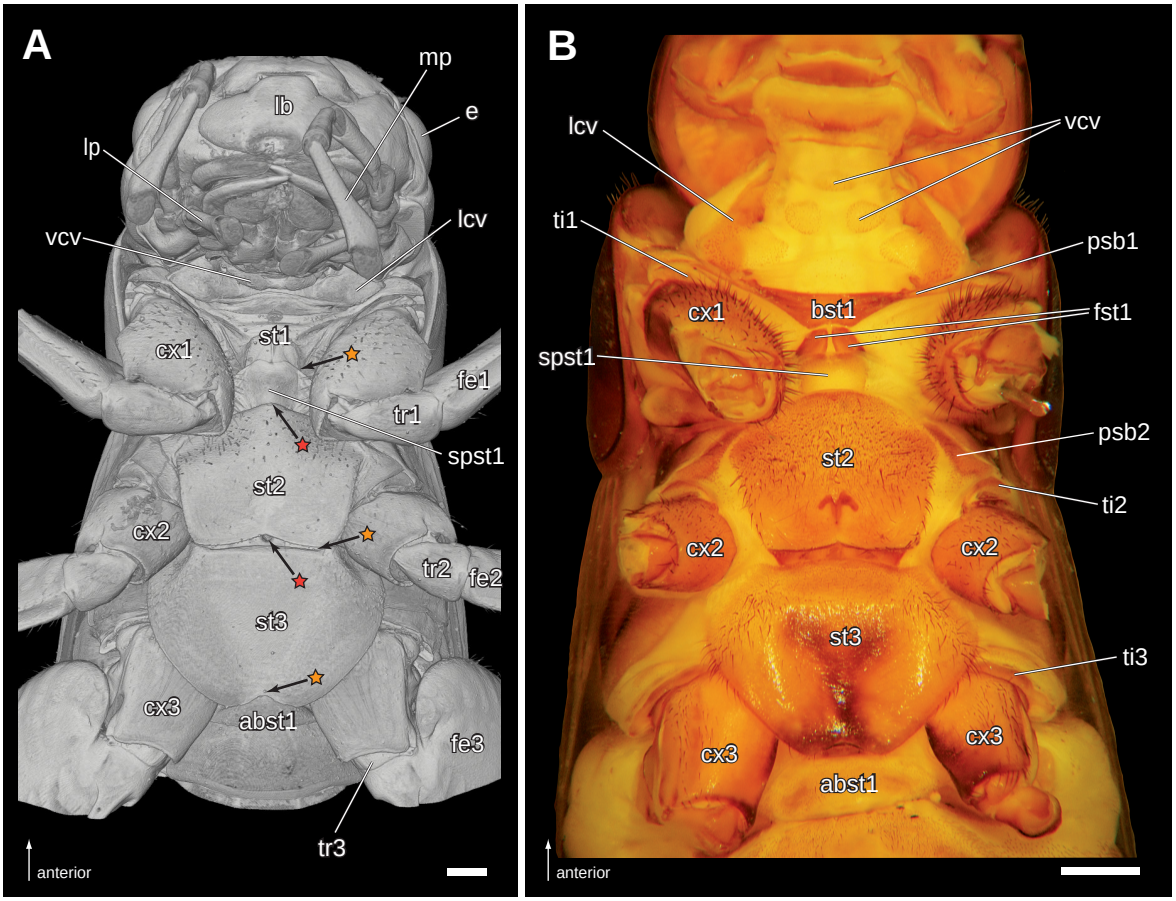

B
fw
hw
sti2
nt1
he
e
mp
lp
est2
em2
sti3
est3
em3
absti1
anterior

Supplementary Plate 8 (see opposite page). Thoracic skeleton of *Gryllus bimaculatus* (Ensifera: Gryllidae). Female. Interior lateral view. Right body half. Photographs. (A) Overview. (B) Detail of neck region and prothorax. Blue asterisks mark pleural ridge. fu1* marks the rounded posterior furcal process of the profurca of the opposite body half. Abbreviations: *absti* first abdominal stigma, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *dcv* dorsal cervical sclerite, *e* compound eye, *em1/2/3* pro-/mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *fw* forewing, *he* head, *lcv* lateral cervical sclerite, *nt1/2/3* pro-/meso-/metanotum, *pcj1* prothoracic pleurocoxal joint, *ph1/2* pro-/mesophragma, *pla2/3* meso-/metathoracic pleural arm, *psb1* prothoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *vcv* ventral cervical sclerite. Scale bars: 1mm.


A
cpl
ph1
ph2
em2
pla2
fw
nt1
he
em3
est2
est3
fu1
sti2
sp1
fu2
sp2
pla3
fu3
absti1
anterior
B
dcv
e
he
ph1
est1
em1
cpl
nt1
fu1
ph2
sti2
est2
em2
lcv
fu1*
fu1
vcv
psb1
est2
sp1
pcj1
anterior

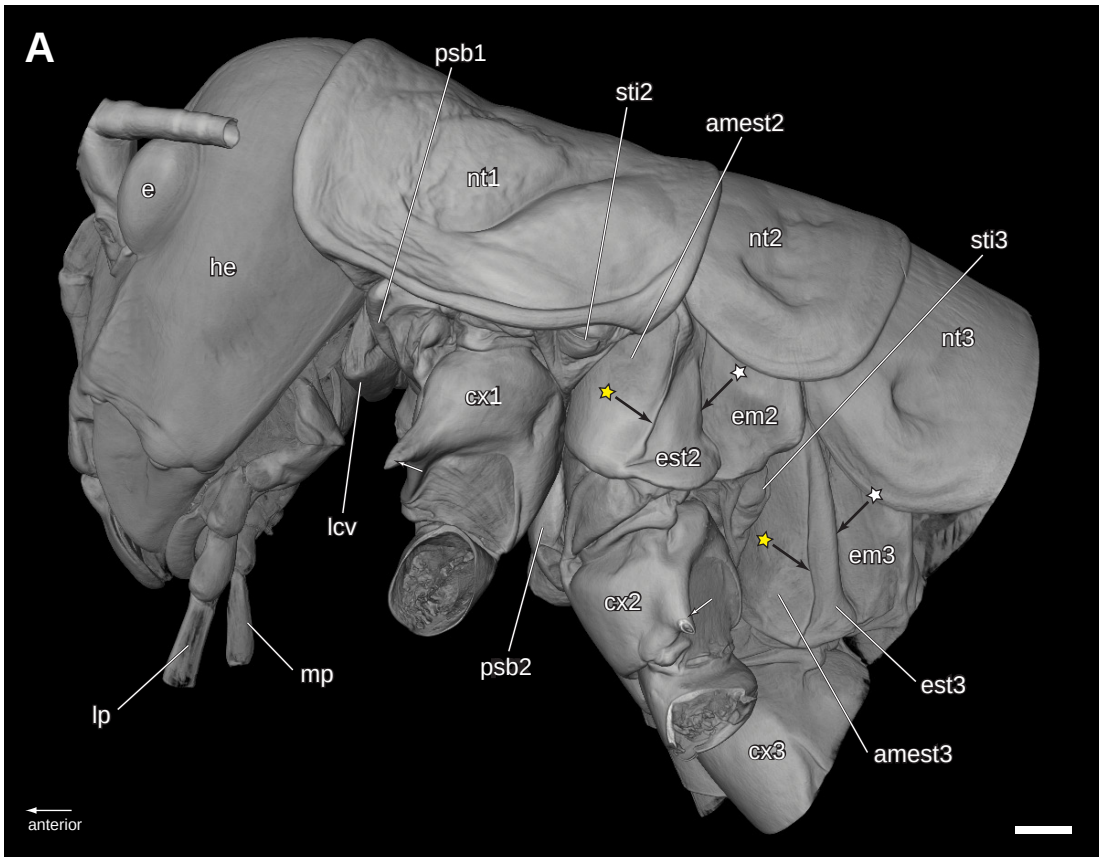


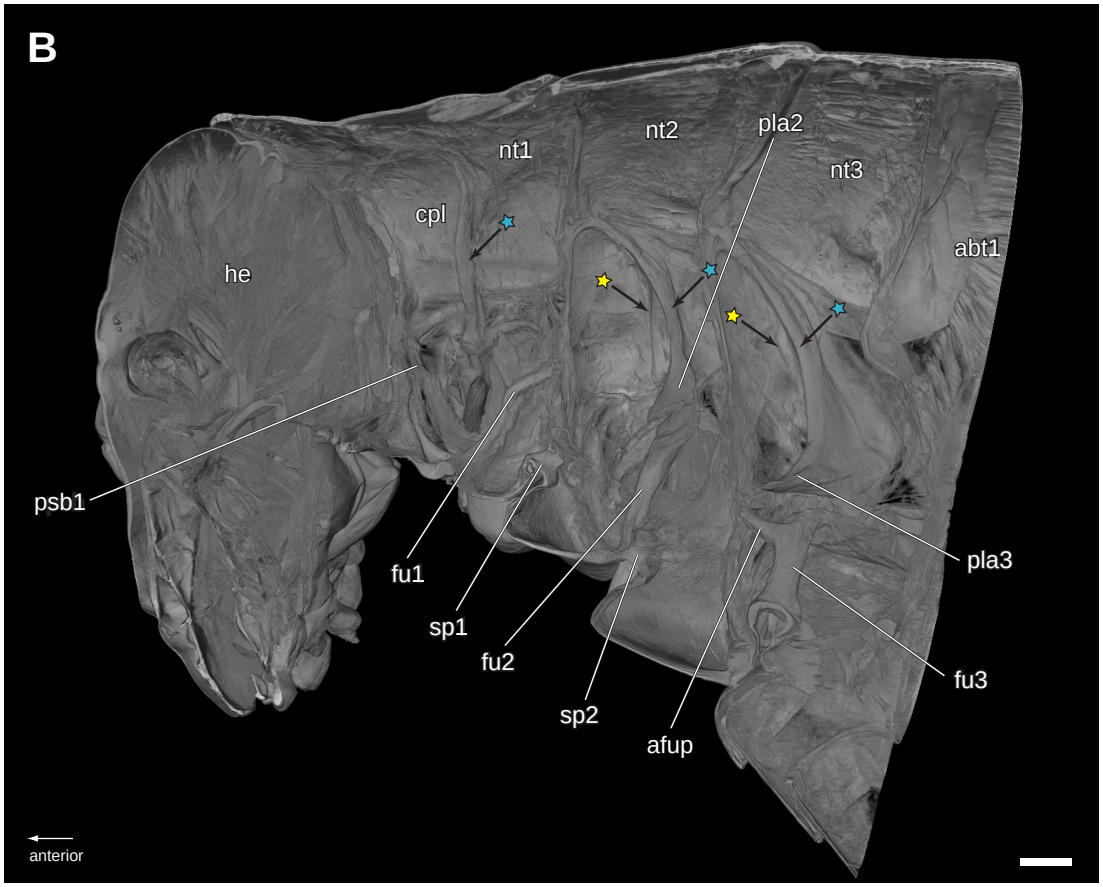
Supplementary Plate 9. Thoracic skeleton of *Gryllus bimaculatus* (Ensifera: Gryllidae). Female. Interior lateral view. Right body half. Three-dimensional volume rendering based on µCT-sections. Blue asterisks mark pleural ridge. The pleural ridge of meso- and metathorax bear the pleural arm projecting into the thoracic cavity. Abbreviations: *cpl* cryptopleura, *em3* metepimeron, *est3* metepisternum, *fu1/2/3* pro-/meso-/metafurca, *fw* forewing, *he* head, *hw* hindwing, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *ph1/2* pro-/mesophragma, *psb1* prothoracic pleurosternal bridge, *sp1/2* pro-/mesospina. Scale bars: 1mm.

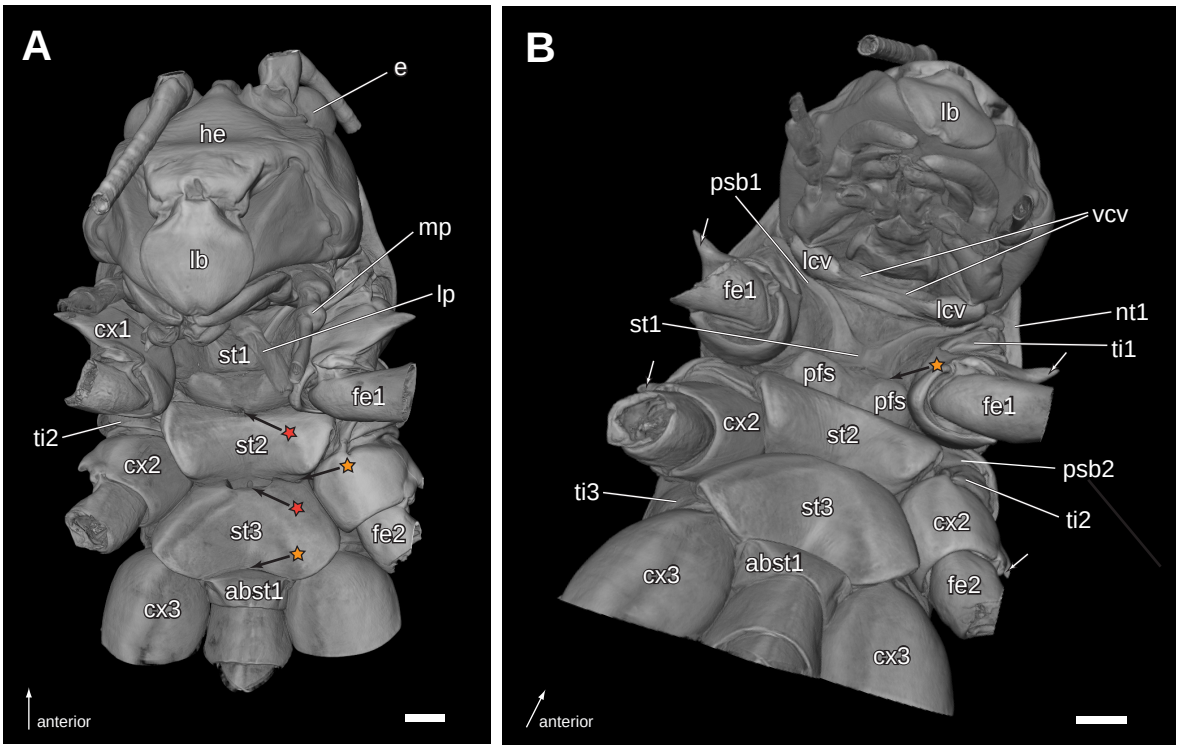


Supplementary Plate 10. Thoracic skeleton of *Gryllus bimaculatus* (Ensifera: Gryllidae). Female. Exterior ventral view. (A) Three-dimensional volume rendering based on µCT-sections. Orange asterisks mark invagination point of pro-/meso-/metafurca. Red asterisks mark invagination point of pro- and mesospina. (B) Photograph. Alkohol-preserved specimen (in Bouin), fixed in an overstretched position to show ventral cervical region. Note paired and freestanding furcasternite of prothorax. Abbreviations: *abst1* first abdominal sternum, *bst1* prothoracic basisternite, *cx1/2/3* pro-/meso-/metacoxa, *em3* metepimeron, *est3* metepisternum, *fe1/2/3* pro-/meso-/metafemur, *fst1* pro-thoracic furcasternite, *he* head, *lcv* lateral cervical slerite, *lb* labrum, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *psb1/2* pro-/mesothoracic pleurosternal bridge, *spst1* prothoracic spinasternite, *st2/3* meso-/metasternum, *ti1/2/3* pro-/meso-/metatrochantin, *tr1/2/3* pro-/meso-/metatrochanter, *vcv* ventral cervical sclerite. Scale bars: 1mm.

Supplementary Plate 11 (see opposite page). Thoracic skeleton of *Hemideina crassidens* (Ensifera: Anostostomatidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Yellow asterisks mark the strongly sclerotized ridge between the episternum and its anterior margin. Blue asterisks mark pleural ridge. White arrows mark coxal spines on pro- and mesocoxa. Abbreviations: *abt1* first abdominal tergum, *afup* anterior furcal process, *amest2/3* anterior margin of mes-/metepisternum , *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *dcv* dorsal cervical sclerite, *e* compound eye, *em1/2/3* pro-/mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lcv* lateral cervical sclerite, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pcj1* prothoracic pleurocoxal joint, *ph1/2* pro-/mesophragma, *pla2/3* meso-/metathoracic pleural arm, *psb1/2* pro-/mesothoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *sti2/3* meso-/metathoraic stigma. Scale bars: 1mm.

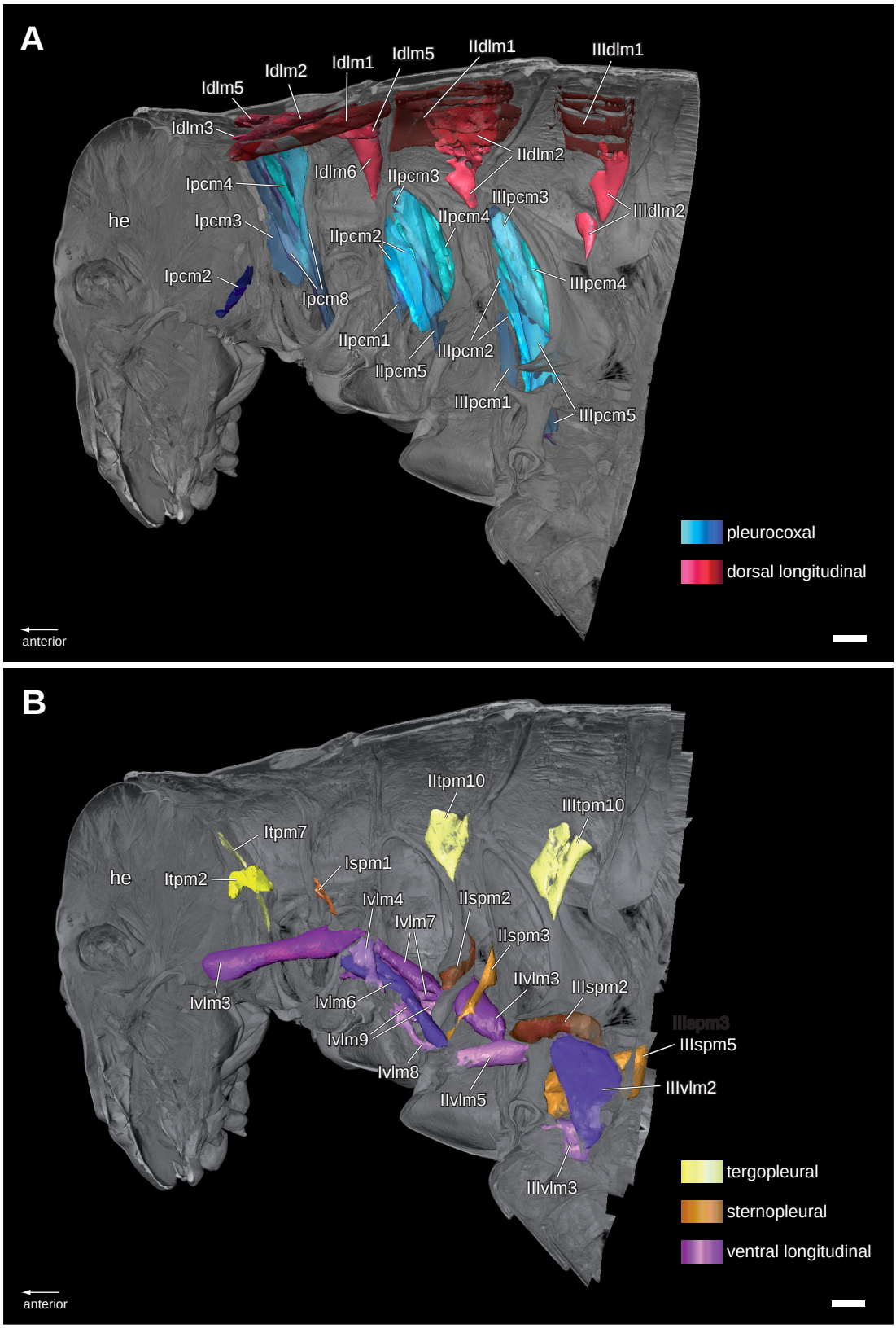

A
psb1
sti2
amest2
nt1
e
he
nt2
sti3
nt3
cx1
em2
est2
lcv
em3
cx2
psb2
mp
est3
lp
cx3
amest3
anterior


B
nt1
nt2
pla2
nt3
cpl
abt1
he
psb1
fu1
sp1
fu2
sp2
afup
pla3
fu3
anterior

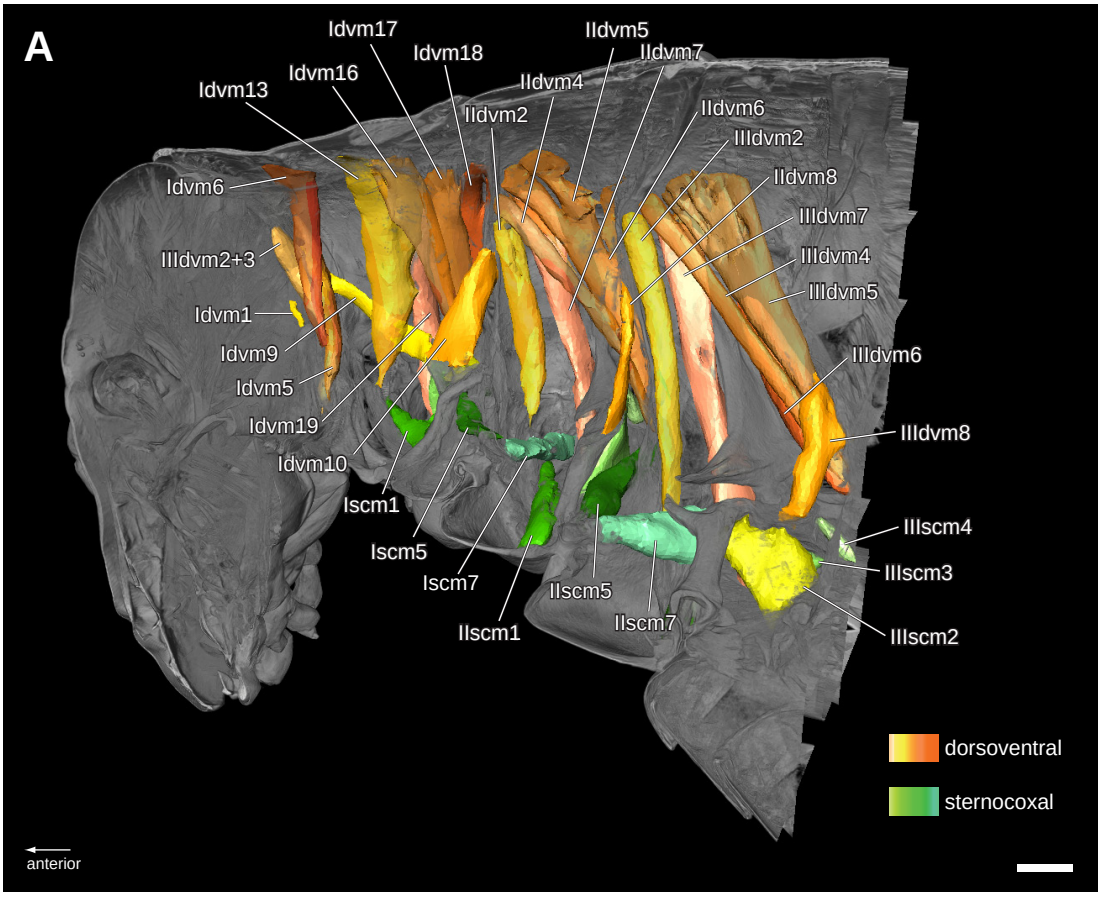


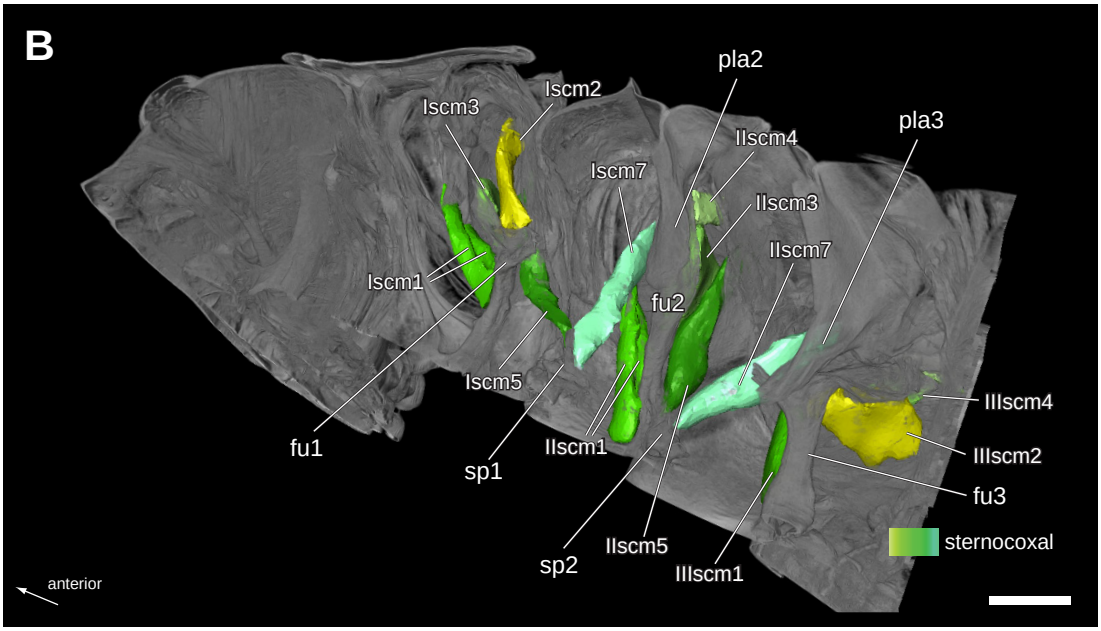
Supplementary Plate 12. Thoracic skeleton of *Hemideina crassidens* (Ensifera: Anostostomatidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior ventral view. (B) Slightly shifted ventral view. Orange asterisks mark invagination point of pro-/meso-/metafurca. Red asterisks mark invagination point of pro- and mesospina. White arrows mark coxal spines on pro- and mesocoxa. Abbreviations: *abst1* first abdominal sternum, *cx1/2/3* pro-/meso-/metacoxa, *em3* metepimeron, *est3* metepisternum, *fe1/2* pro-/mesofemur, *he* head, *lcv* lateral cervical slerite, *lb* labrum, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pfs* postfurasternite, *psb1/2* pro-/mesothoracic pleurosternal bridge, *spst1* prothoracic spinasternite, *st1/2/3* pro-/meso-/metasternum, *ti1/2/3* pro-/meso-/metatrochantin, *vcv* ventral cervical sclerite. Scale bars: 1mm.

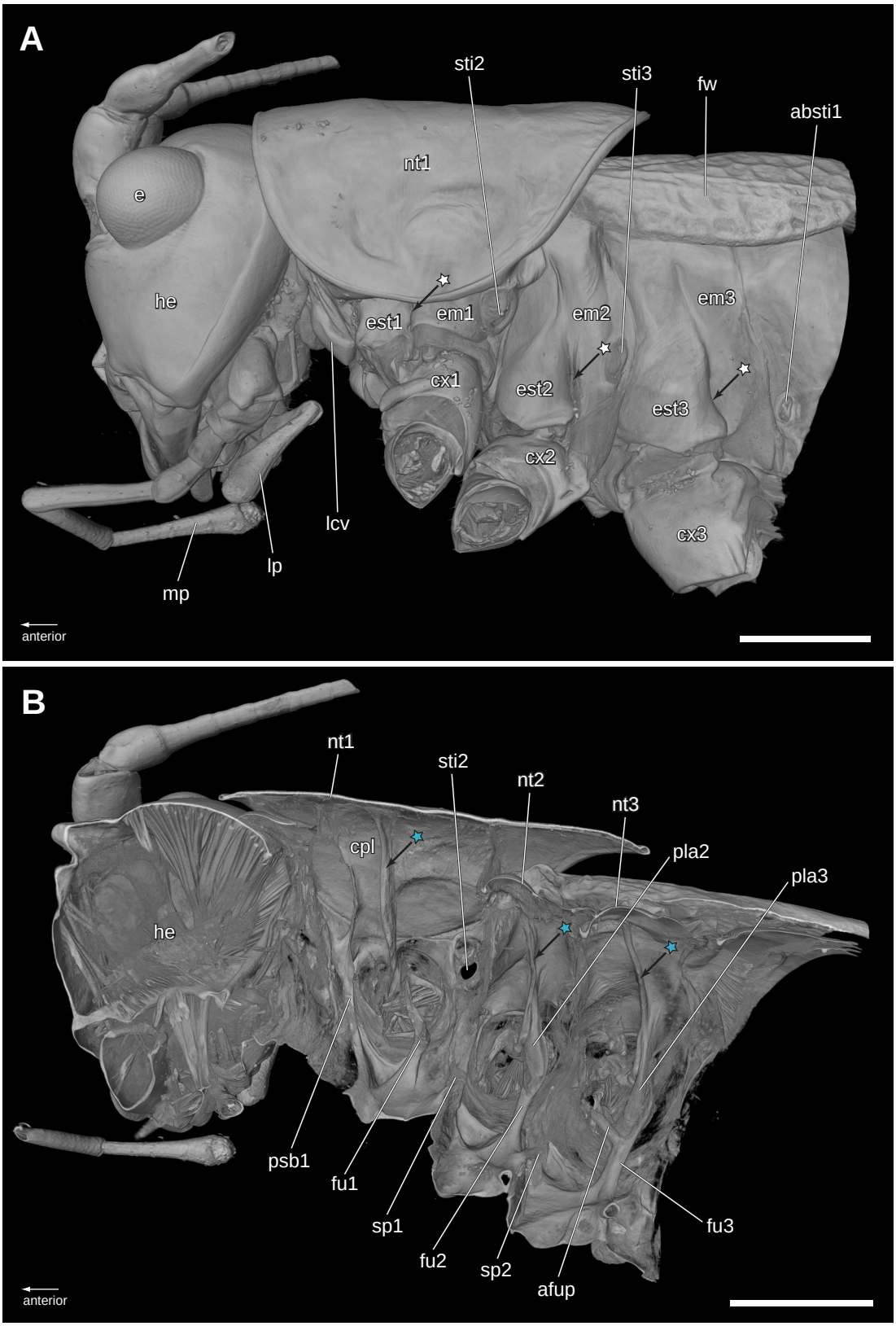
Supplementary Plate 13 (see opposite page). Thoracic musculature of *Hemideina crassidens* (Ensifera: Anostostomatidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Dorsal longitudinal muscles (dlm) and pleurocoxal muscles (pcm). (B) Tergopleural muscles (tpm), sternopleural muscles (spm) and ventral longitudinal muscles (vlm). Abbreviations: *he* head. Scale bars: 1mm.

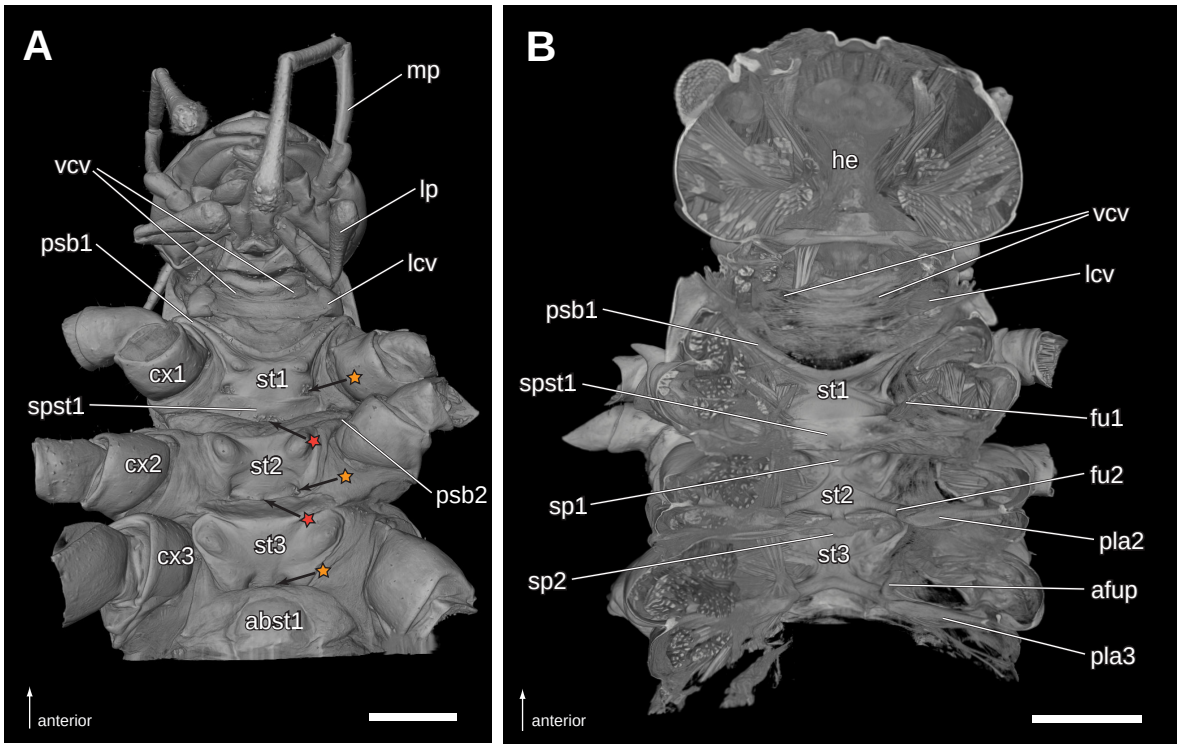

A
Idlm5
Idlm2
Idlm1
Idlm5
IIdlm1
IIIdlm1
Idlm3
IIdlm2
Idlm6
IIpcm3
Ipcm4
IIIpcm3
IIIdlm2
he
Ipcm3
IIpcm4
IIpcm2
Ipcm2
IIIpcm4
Ipcm8
IIpcm1
IIIpcm2
IIpcm5
IIIpcm1
IIIpcm5
pleurocoxal
dorsal longitudinal
anterior
B
IItpm10
IIItpm10
Itpm7
Ispm1
he
Itpm2
Ivlm4
IIspm2
Ivlm7
IIspm3
IIvlm3
IIIspm2
Ivlm3
Ivlm6
IIIspm5
Ivlm9
IIIvlm2
Ivlm8
IIvlm5
IIIvlm3
tergopleural
sternopleural
ventral longitudinal
anterior

Supplementary Plate 14 (see opposite page). Thoracic musculature of *Hemideina crassidens* (Ensifera: Anostostomatidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. (A) Interior lateral view. Dorsoventral muscles (dvm) and sternocoxal muscles (scm). (B) Interior ventrolaterlal view. Sternocoxal muscles (scm). Abbreviations: *fu1/2/3* pro-/meso-/metafurca, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.


A
ldvm17
ldvm18
ldvm16
ldvm13
IIdvm5
IIdvm7
IIdvm4
IIdvm2
IIdvm6
IIIdvm2
IIdvm8
IIIdvm7
IIIdvm4
IIIdvm5
ldvm6
IIIdvm2+3
ldvm1
ldvm9
ldvm5
ldvm19
ldvm10
lscm1
lscm5
lscm7
IIscm1
IIscm5
IIscm7
IIIdvm6
IIIdvm8
IIIscm4
IIIscm3
IIIscm2
dorsoventral
sternocoxal
anterior

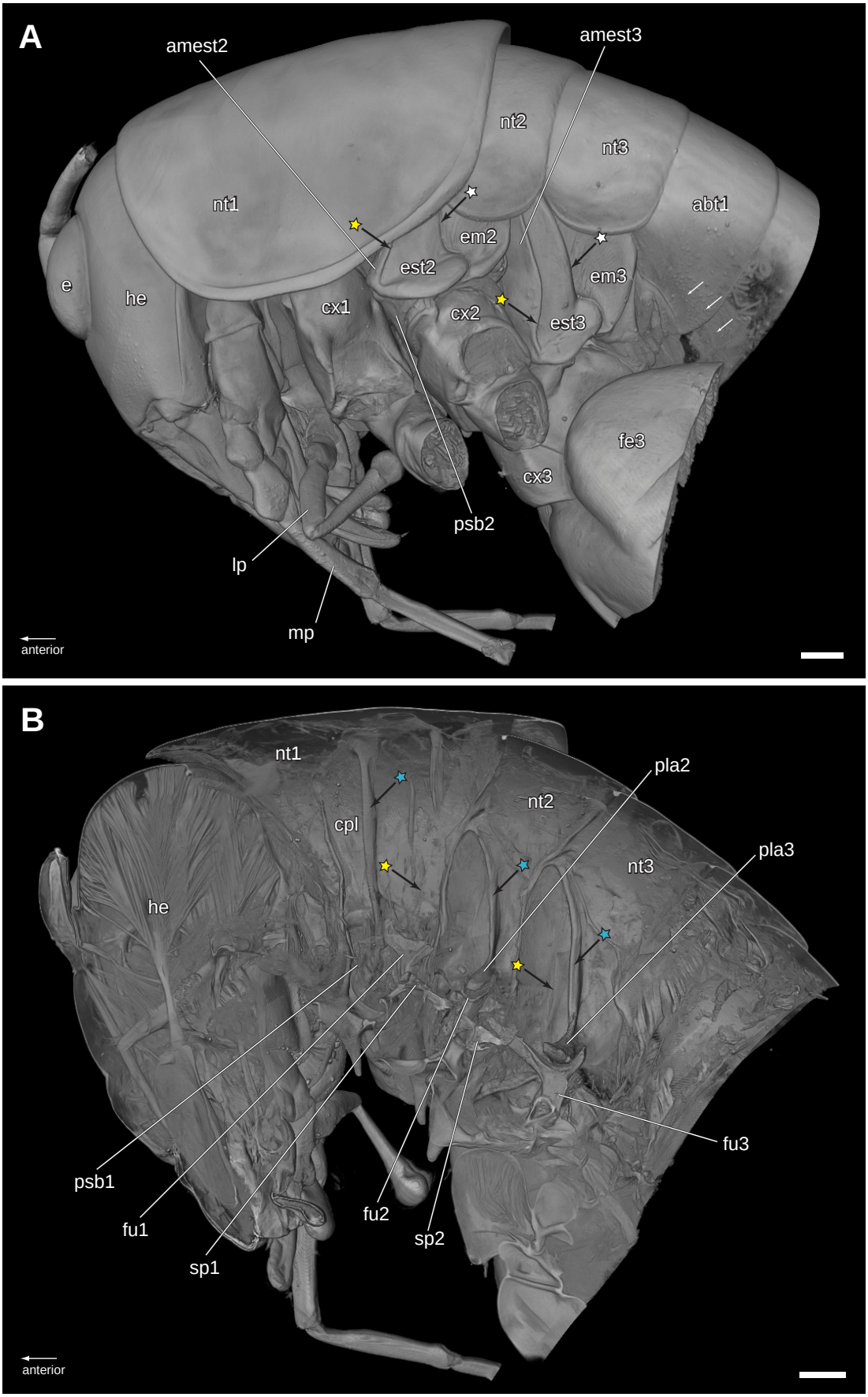

B
pla2
lscm3
lscm2
pla3
IIscm4
lscm7
IIscm3
IIscm7
lscm1
fu2
lscm5
IIIscm4
IIIscm2
fu1
sp1
IIscm1
fu3
sternocoxal
sp2
IIscm5
IIIscm1
anterior

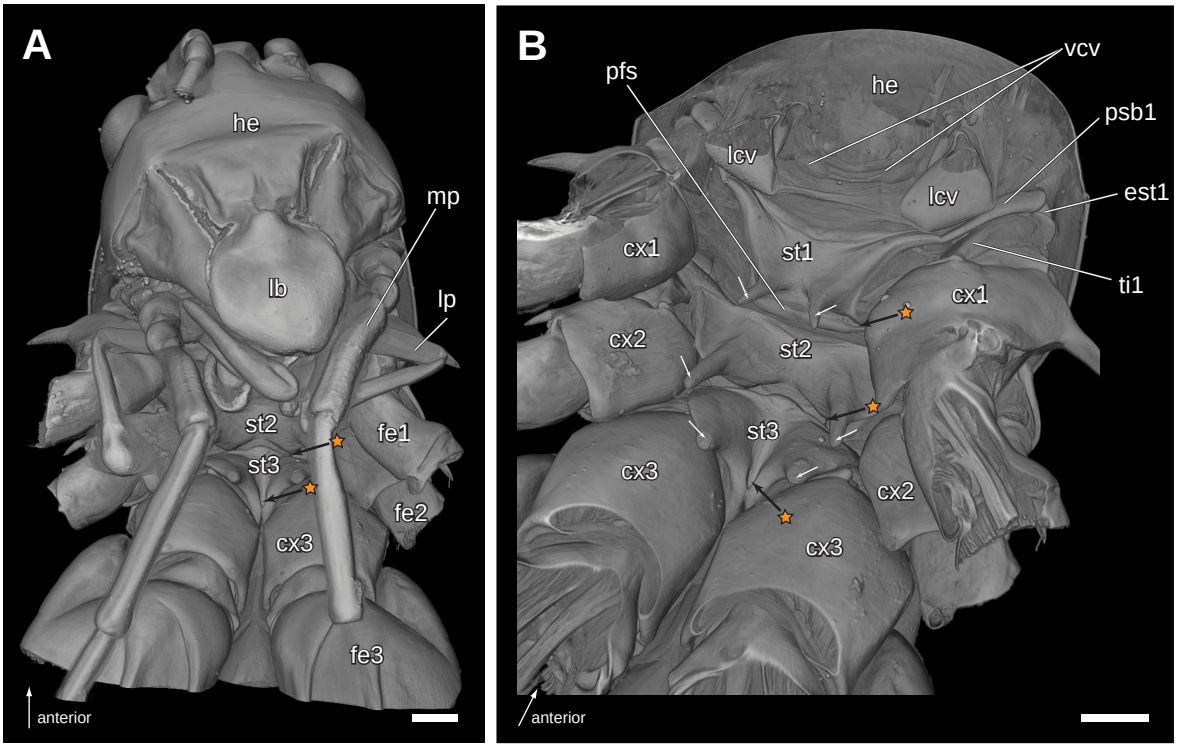

A
sti2
sti3
fw
absti1
nt1
e
he
est1
em1
em2
em3
cx1
est2
est3
cx2
lcv
cx3
lp
mp
anterior
B
nt1
sti2
nt2
nt3
cpl
pla2
pla3
he
psb1
fu1
sp1
fu2
sp2
afup
fu3
anterior



Supplementary Plate 15. Thoracic skeleton of *Meconema meridionale* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior ventral view. Orange asterisks mark invagination point of pro-/meso-/metafurca. Red asterisks mark invagination point of pro- and mesospina. (B) Interior ventral view. Abbreviations: *abst1* first abdominal sternum, *afup* anterior furcal process, *cx1/2/3* pro-/meso-/metacoxa, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lcv* lateral cervical slerite, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm, *psb1/2* pro-/mesothoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *spst1* prothoracic spinasternite, *st1/2/3* pro-/meso-/metasternum, *vcv* ventral cervical sclerite. Scale bars: 1mm.

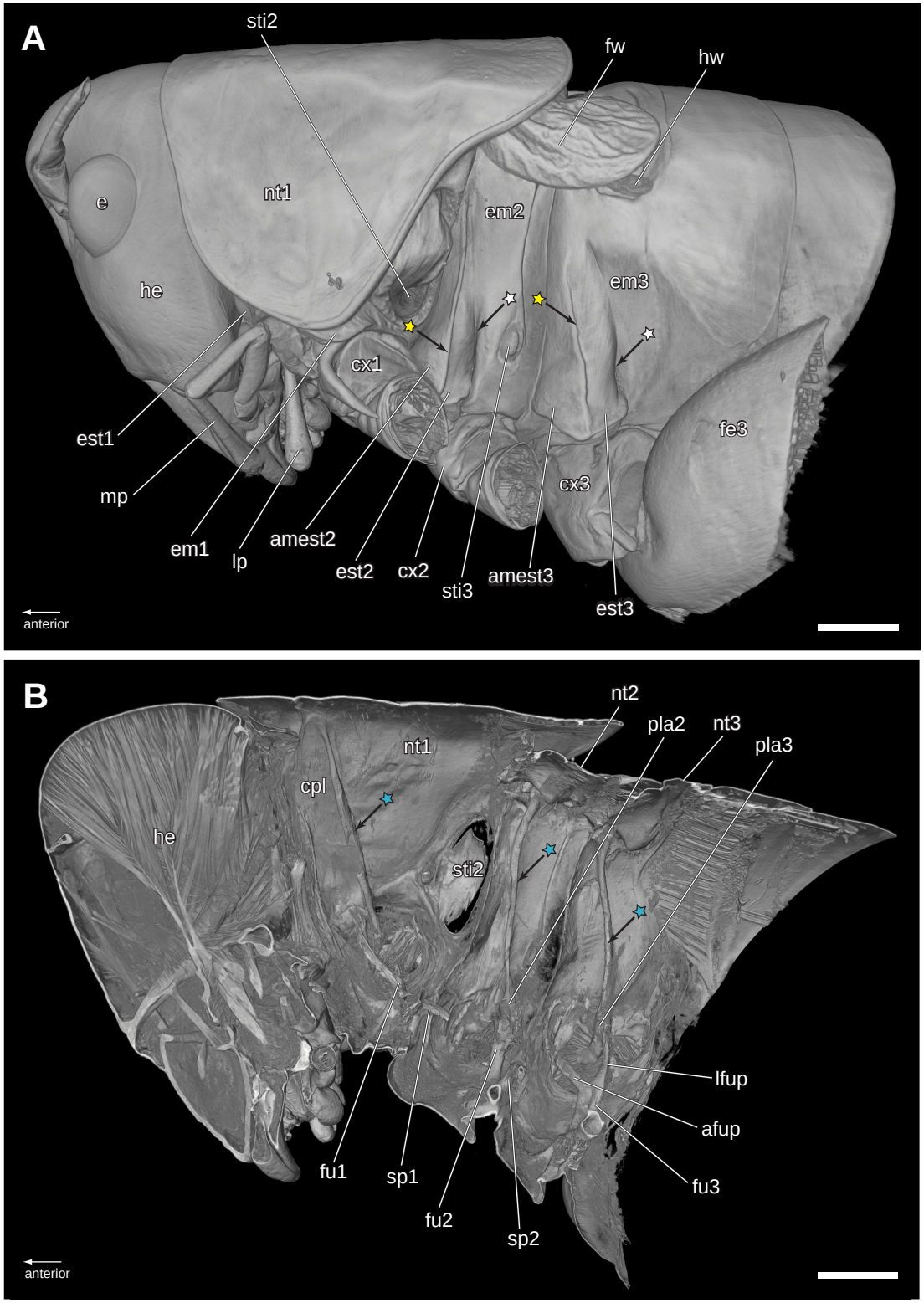
Supplementary Plate 16 (see opposite page). Thoracic skeleton of *Meconema meridionale* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Yellow asterisks mark the strongly sclerotized ridge between the episternum and its anterior margin. Blue asterisks mark pleural ridge. White arrows mark coxal spines on pro- and mesocoxa. Abbreviations: *absti1* first abdominal stigma, *abt1* first abdominal tergum, *afup* anterior furcal process, *amest2/3* anterior margin of mes-/metepisternum , *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *dcv* dorsal cervical sclerite, *e* compound eye, *em1/2/3* pro-/mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *fw* forewing, *he* head, *lcv* lateral cervical sclerite, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm, *psb1* prothoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *sti2/3* meso-/metathoraic stigma. Scale bars: 1mm.

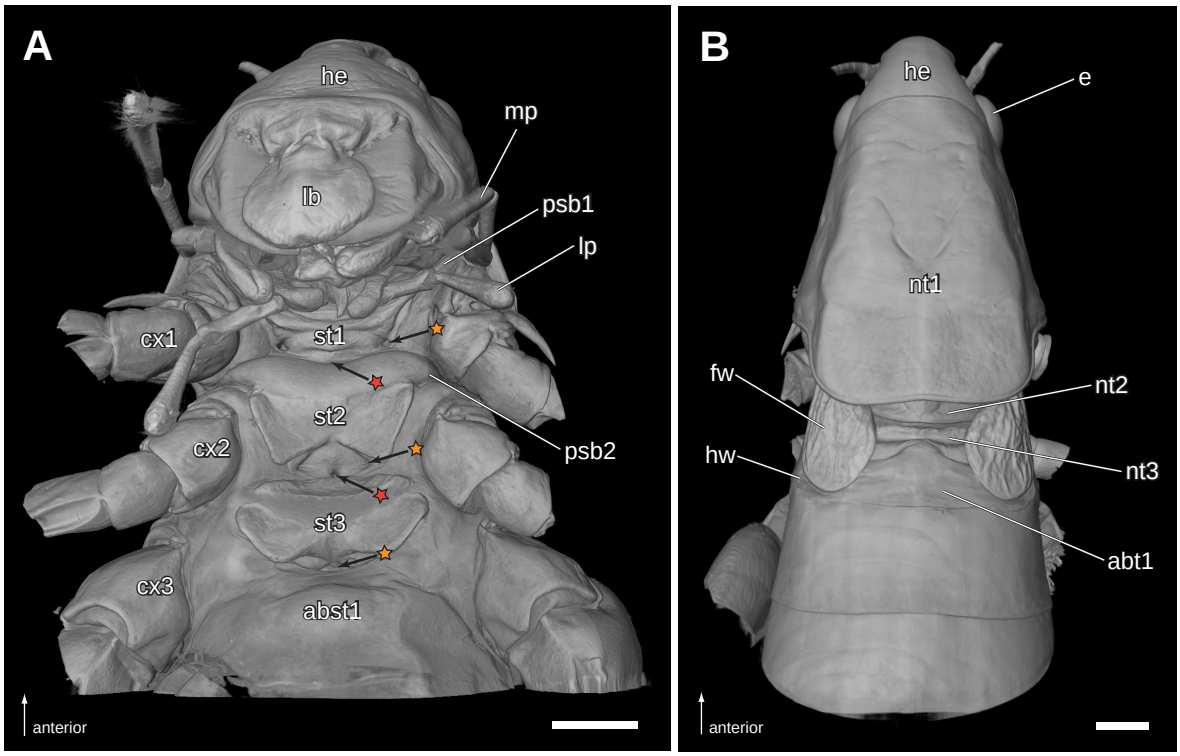

A
amest2
amest3
nt2
nt3
nt1
abt1
em2
est2
em3
e
he
cx1
cx2
est3
fe3
cx3
psb2
lp
mp
anterior
B
nt1
pla2
nt2
cpl
pla3
nt3
he
psb1
fu3
fu1
fu2
sp2
sp1
anterior



Supplementary Plate 17. Thoracic skeleton of *Papuaistus* sp. (Ensifera: Anostostomatidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior ventral view. (B) Slightly shifted ventral view. Head and mouthparts clipped off to show ventral cervical region. Orange asterisks mark invagination point of pro-/meso-/metafurca. Invagination points of pro- and mesospina hidden due to concave bent of ventral thoracic side. White arrows mark sternal spines at pro-/meso-/metasternum. Abbreviations: *cx1/2/3* pro-/meso-/metacoxa, *est1* proepisternum, *fe1/2/3* pro-/meso-/metafemur, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lb* labrum, *lcv* lateral cervical slerite, *lp* labial palp, *mp* maxillary palp, *pfs* postfurcasternite, *psb1* prothoracic pleurosternal bridge, *st1/2/3* pro-/meso-/metasternum, *ti1* protrochantin, *vcv* ventral cervical sclerite. Scale bars: 1mm.

Supplementary Plate 18 (see opposite page). Thoracic skeleton of *Papuaistus* sp. (Ensifera: Anostostomatidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Yellow asterisks mark the strongly sclerotized ridge between the episternum and its anterior margin. Blue asterisks mark pleural ridge. White arrows mark denticles on the first and second abdominal tergites that form part of the femoro-abdominal stridulatory apparatus. Abbreviations: *abt1* first abdominal tergum, *amest2/3* anterior margin of mes-/metepisternum, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *em2/3* mes-/metepimeron, *est2/3* mes-/metepisternum, *fe3* metafemur, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lcv* lateral cervical sclerite, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm, *psb1/2* pro-/mesothoracic pleurosternal bridge, *sp1/2* pro-/mesospina. Scale bars: 1mm.

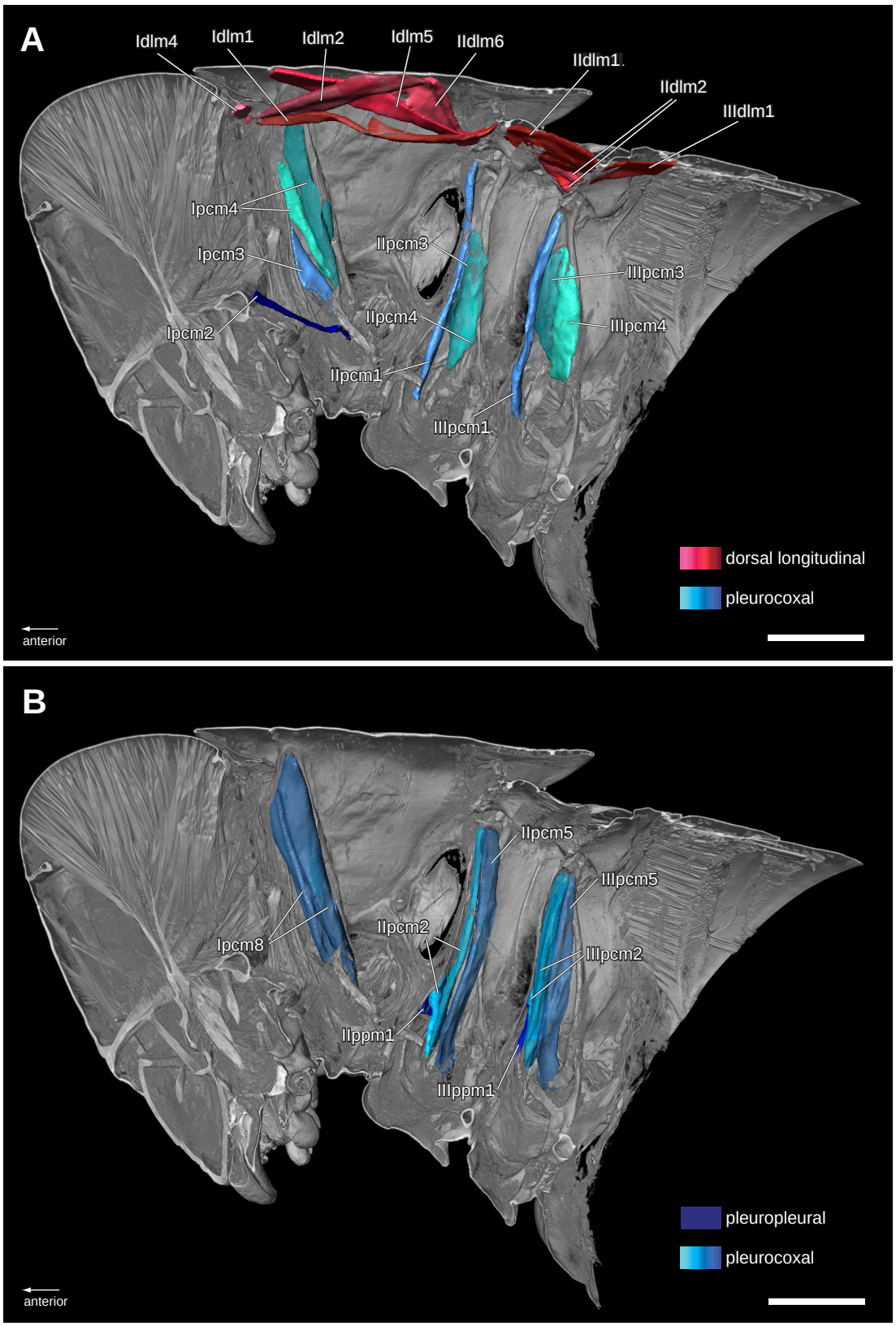

A
sti2
fw
hw
e
nt1
em2
he
em3
cx1
est1
fe3
mp
cx3
em1
lp
amest2
est2
cx2
sti3
amest3
est3
anterior
B
nt2
pla2
nt3
pla3
nt1
cpl
he
sti2
lfup
afup
fu3
fu1
sp1
fu2
sp2
anterior



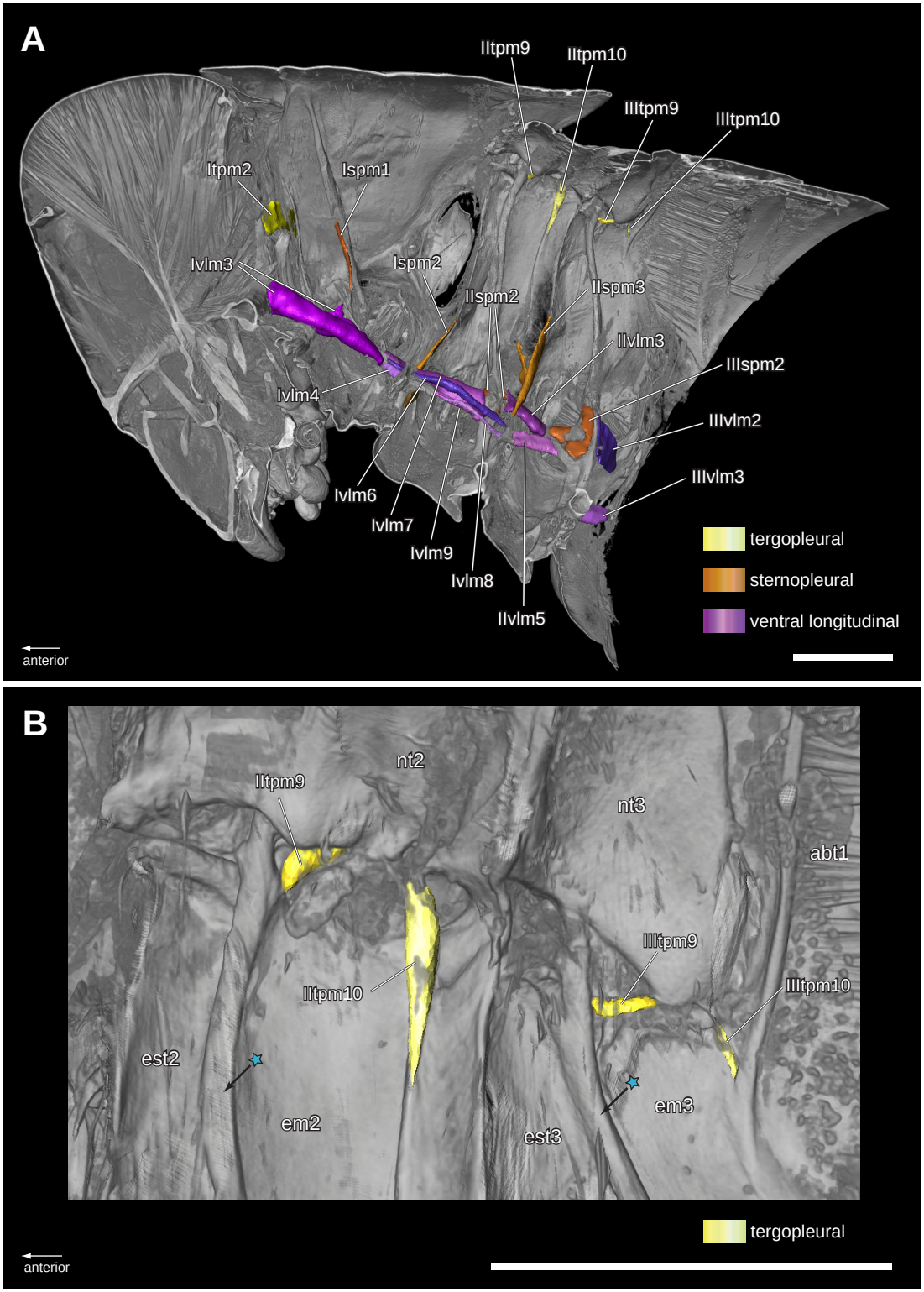
Supplementary Plate 19. Thoracic skeleton of *Pholidoptera griseoaptera* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior ventral view. Orange asterisks mark invagination points of pro-/meso-/metafurca. Red asterisks mark invagination points of pro- and mesospina. (B) Exterior dorsal view. Abbreviations: *abt1* first abdominal tergum, *abst1* first abdominal sternum, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *fw* forewing, *he* head, *hw* hindwing, *lb* labrum, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *psb1/2* pro-/mesothoracic pleurosternal bridge, *st1/2/3* pro-/meso-/metasternum. Scale bars: 1mm.

Supplementary Plate 20 (see opposite page). Thoracic skeleton of *Pholidoptera griseoaptera* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Yellow asterisks mark the strongly sclerotized ridge between the episternum and its anterior margin. Blue asterisks mark pleural ridge. Abbreviations: *abt1* first abdominal tergum, *afup* anterior furcal process, *amest2/3* anterior margin of mes-/metepisternum, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *em1/2/3* pro-/mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fe3* metafemur, *fu1/2/3* pro-/meso-/metafurca, *fw* forewing, *he* head, *hw* hindwing, *lfup* lateral furcal process, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.

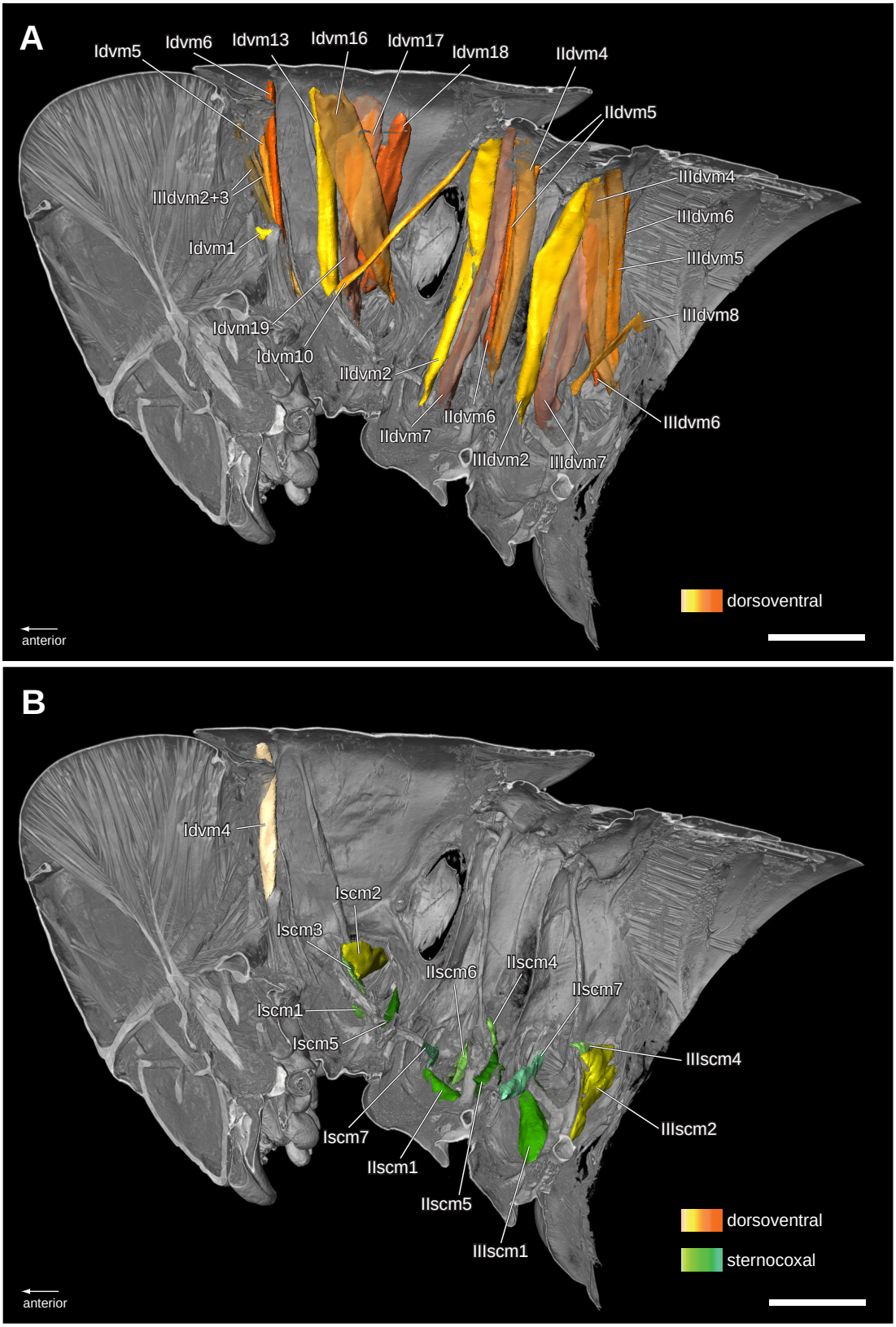
Supplementary Plate 21 (see opposite page). Thoracic musculature of *Pholidoptera griseoaptera* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Dorsal longitudinal muscles (dlm) and pleurocoxal muscles (pcm) (in part). (B) Pleuropleural muscles (ppm) and pleurocoxal muscles (pcm) (in part). Scale bars: 1mm.

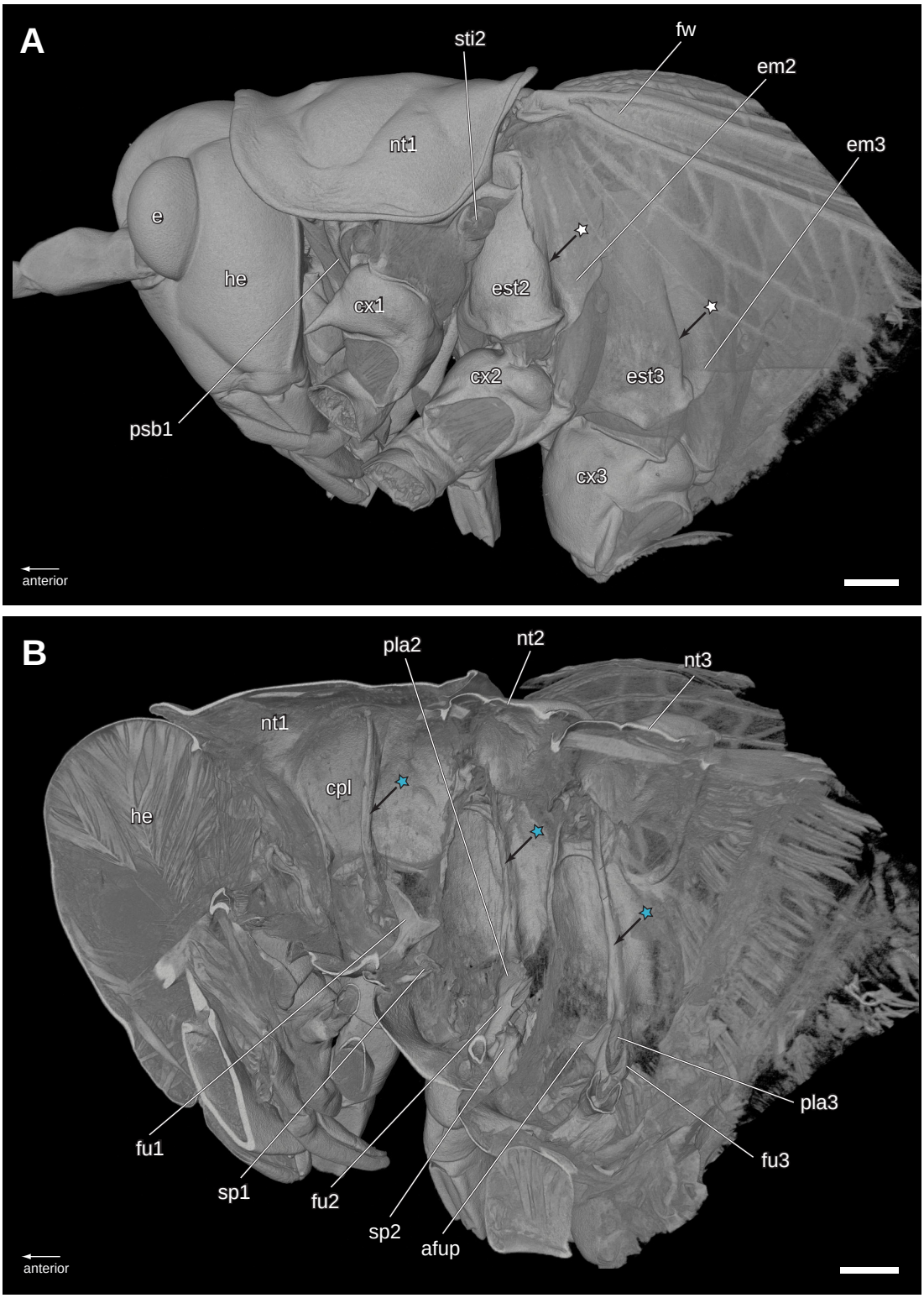

A
Idlm4
Idlm1
Idlm2
Idlm5
IIdlm6
IIdlm1
IIdlm2
IIIdlm1
Ipcm4
Ipcm3
Ipcm2
IIpcm3
IIpcm4
IIpcm1
IIIpcm3
IIIpcm4
IIIpcm1
dorsal longitudinal
pleurocoxal
anterior
B
IIpcm5
IIIpcm5
Ipcm8
IIpcm2
IIIpcm2
IIppm1
IIIppm1
pleuropleural
pleurocoxal
anterior

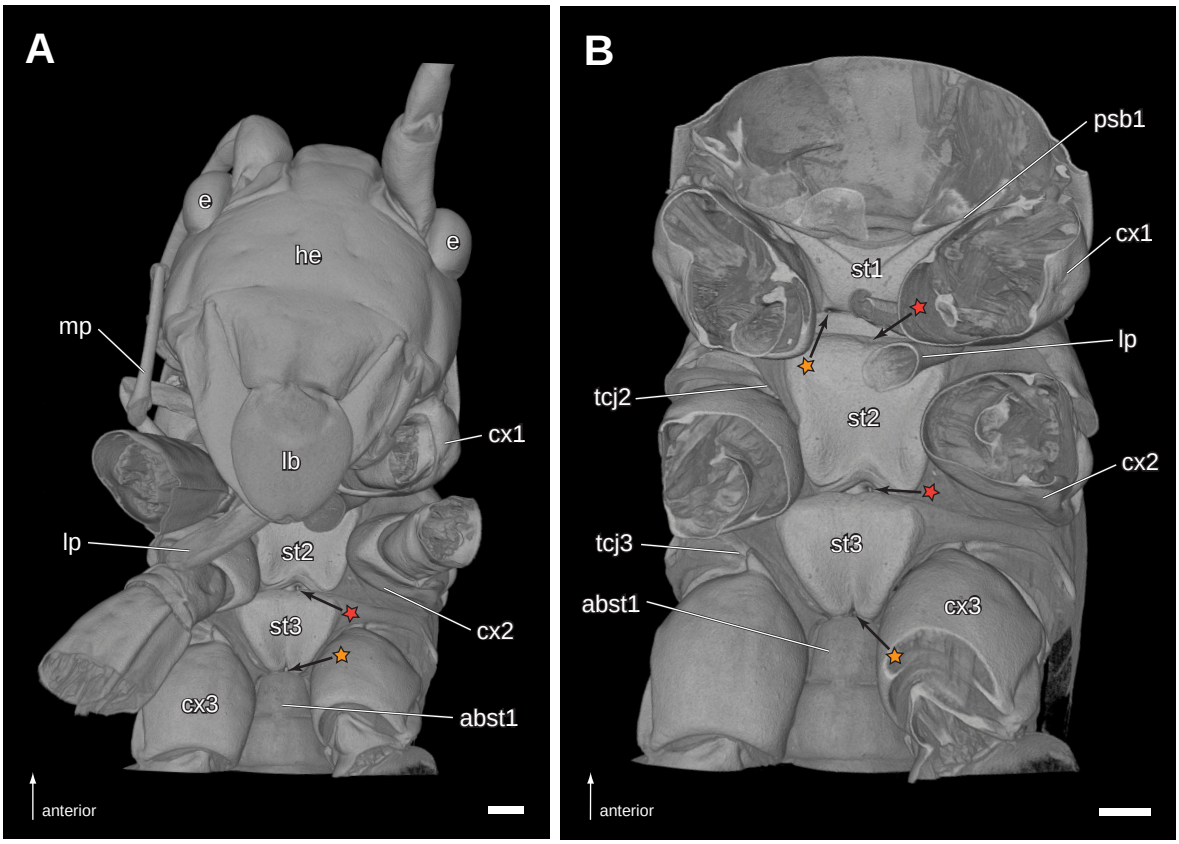
Supplementary Plate 22 (see opposite page). Thoracic musculature of *Pholidoptera griseoaptera* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Tergopleural muscles (tpm), sternopleural muscles (spm) and ventral longitudinal muscles (vlm). (B) Slightly shifted interior lateral view of pterothorax. Tergopleural muscles (tpm) of pterothorax. Blue asterisks mark pleural ridge. Abbreviations: *abt* first abdominal tergum, *em2/3* mes-/metepimeron, *est2/3* mes-/metepisternum, *nt2/3* meso-/metanotum. Scale bars: 1mm.


A
IItpm9
IItpm10
IIItpm9
IIItpm10
Itpm2
Ispm1
Ispm2
IIspm2
IIspm3
Ivlm3
IIvlm3
IIIspm2
Ivlm4
IIIvlm2
IIIvlm3
Ivlm6
Ivlm7
Ivlm9
Ivlm8
IIvlm5
tergopleural
sternopleural
ventral longitudinal
anterior
B
nt2
IItpm9
nt3
abt1
IIItpm9
IItpm10
IIItpm10
est2
em2
em3
est3
tergopleural
anterior

Supplementary Plate 23 (see opposite page). Thoracic musculature of *Pholidoptera griseoaptera* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Dorsoventral muscles (dvm) and sternocoxal muscles (scm). (B) Idvm4 (M. pronoto-cervicalis lateralis)and sternocoxal muscles (scm). Scale bars: 1mm.


A
Idvm5
Idvm6
Idvm13
Idvm16
Idvm17
Idvm18
IIdvm4
IIdvm5
IIIdvm4
IIIdvm2+3
IIIdvm6
Idvm1
IIIdvm5
IIIdvm8
Idvm19
Idvm10
IIdvm2
IIdvm6
IIIdvm6
IIdvm7
IIIdvm2
IIIdvm7
dorsoventral
anterior
B
Idvm4
Iscm2
Iscm3
IIscm6
IIscm4
IIscm7
Iscm1
Iscm5
IIIscm4
IIIscm2
Iscm7
IIscm1
IIscm5
IIIscm1
dorsoventral
sternocoxal
anterior

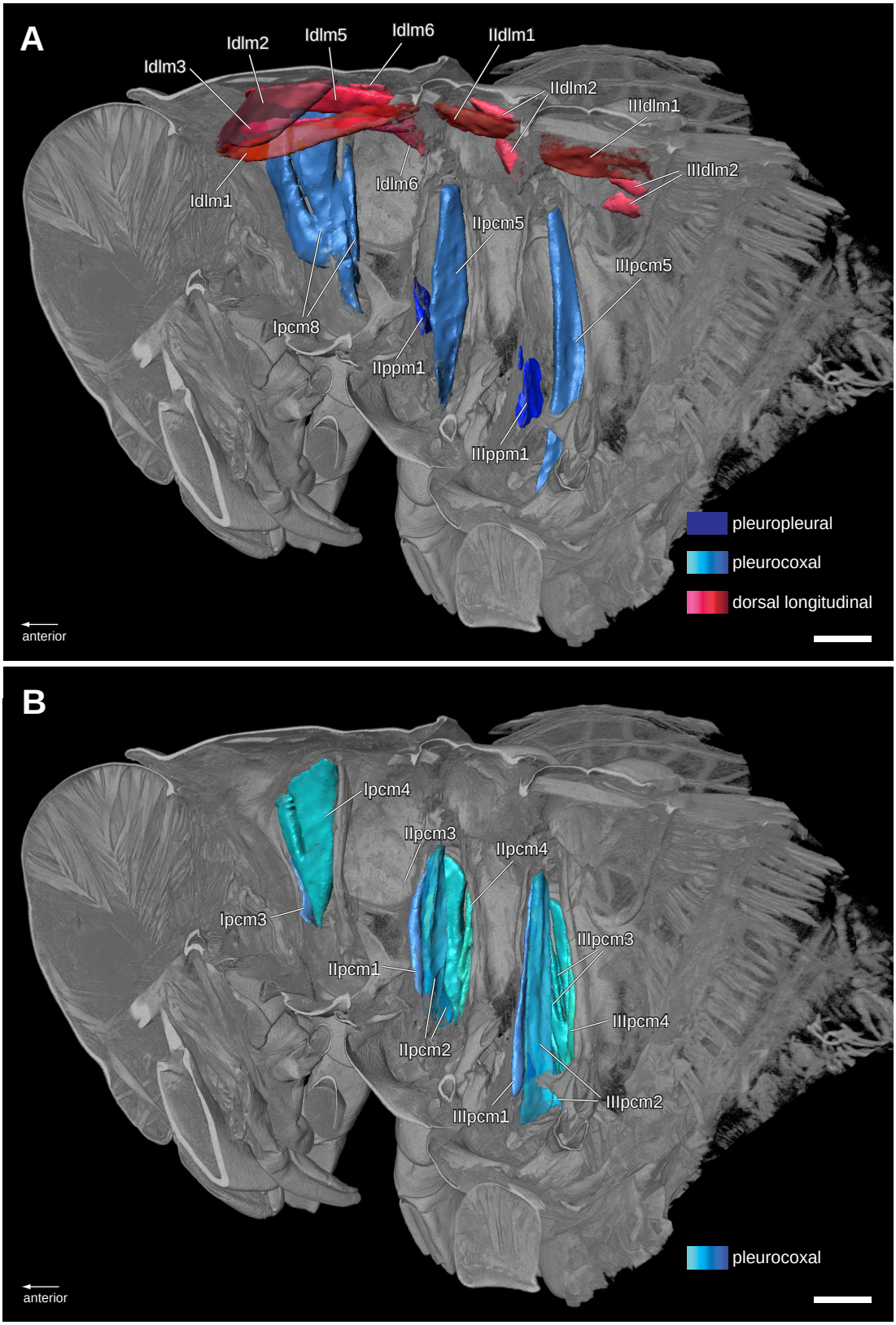

A
sti2
fw
em2
em3
nt1
e
he
cx1
est2
cx2
est3
psb1
cx3
anterior
B
pla2
nt2
nt3
nt1
cpl
he
fu1
sp1
fu2
sp2
afup
pla3
fu3
anterior

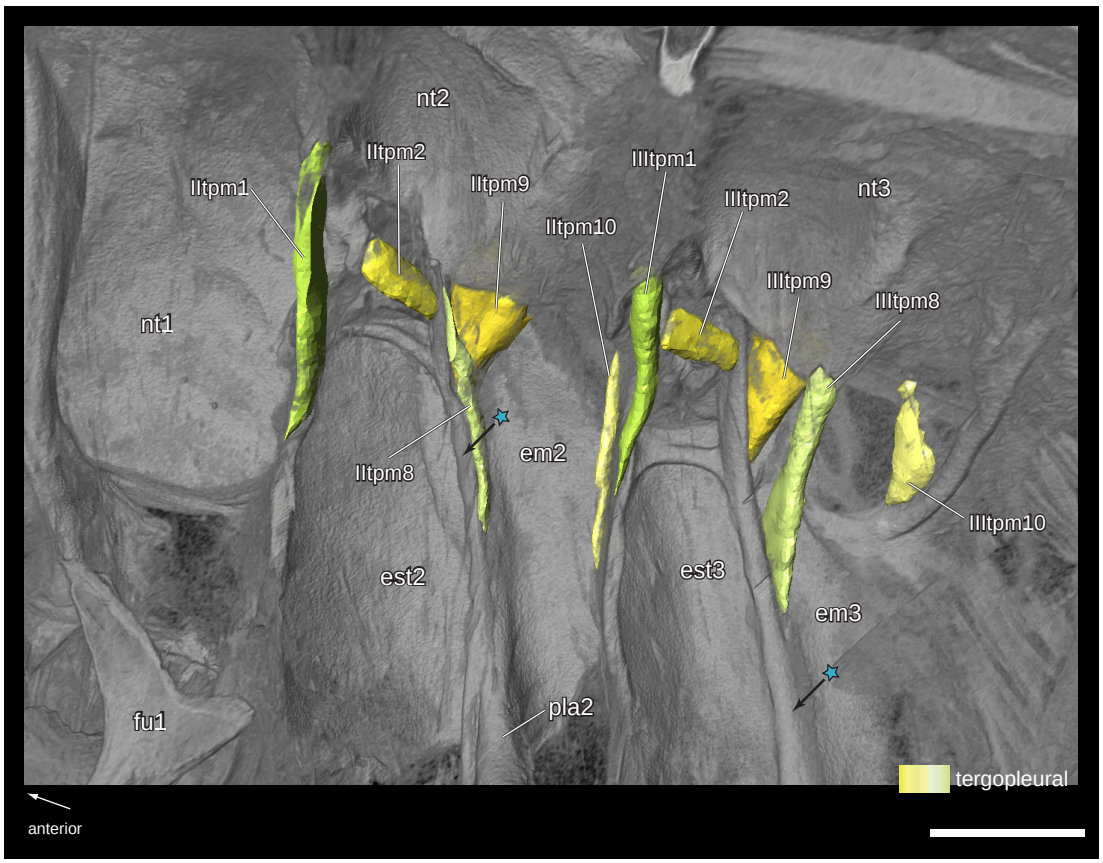


Supplementary Plate 24. Thoracic skeleton of *Prosopogryllacris* sp. (Ensifera: Gryllacrididae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior ventral view. (B) Exterior ventral view. Head and mouthparts clipped off to show ventral cervical region. Orange asterisks mark invagination points of pro- and metafurca. Furcal pit of mesofurca hidden by mesosternum. Red asterisks mark invagination points of pro- and mesospina. Abbreviations: *abst1* first abdominal sternum, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *he* head, *lb* labrum, *lp* labial palp, *mp* maxillary palp, *psb1* prothoracic pleurosternal bridge, *st1/2/3* pro-/meso-/metasternum, *tcj2/3* meso-/metathoracic trochantino-coxal joint. Scale bars: 1mm.

Supplementary Plate 25 (see opposite page). Thoracic skeleton of *Prosopogryllacris* sp. (Ensifera: Gryllacrididae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Blue asterisks mark pleural ridge. Abbreviations: *afup* anterior furcal process, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *em2/3* mes-/metepimeron, *est2/3* mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *fw* forewing, *he* head, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm, *psb1* prothoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *sti2* mesothoracic stigma. Scale bars: 1mm.

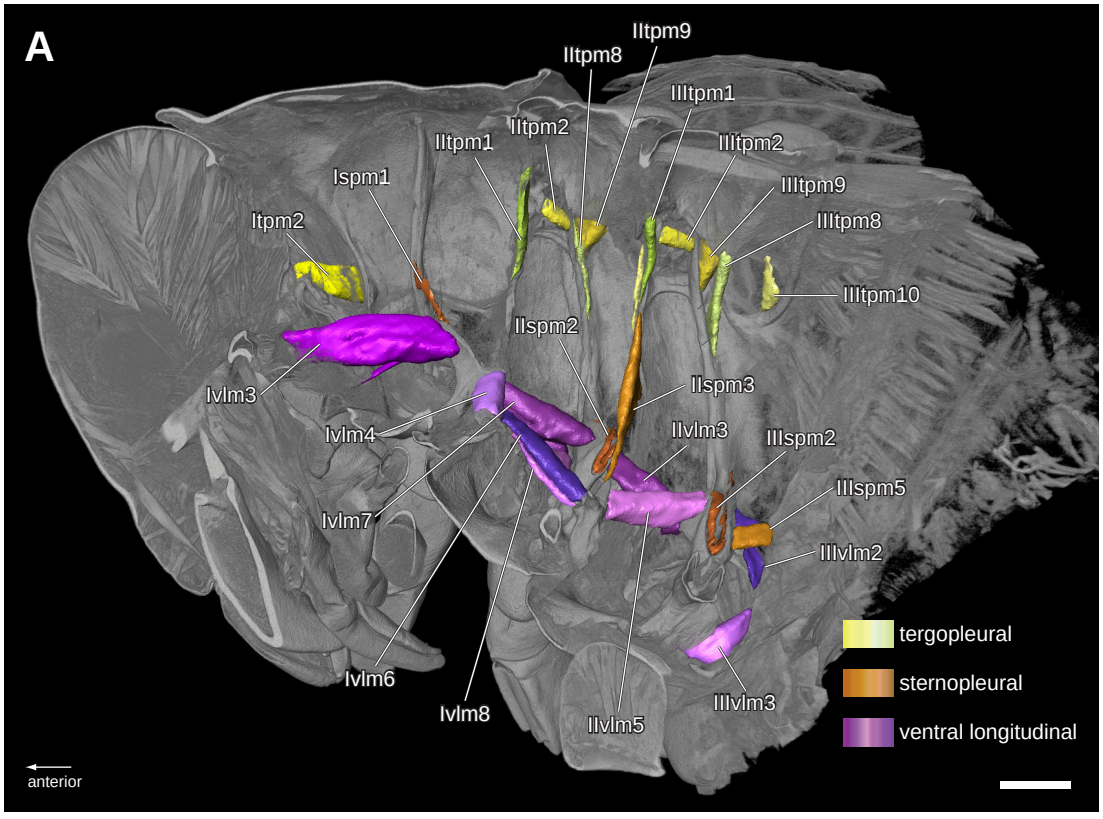
Supplementary Plate 26 (see opposite page). Thoracic musculature of *Prosopogryllacris* sp. (Ensifera: Gryllacrididae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Dorsal longitudinal muscles (dlm), pleuropleural muscles (ppm) and pleurocoxal muscles (pcm) (in part). (B) Pleurocoxal muscles (pcm) (in part). Scale bars: 1mm.

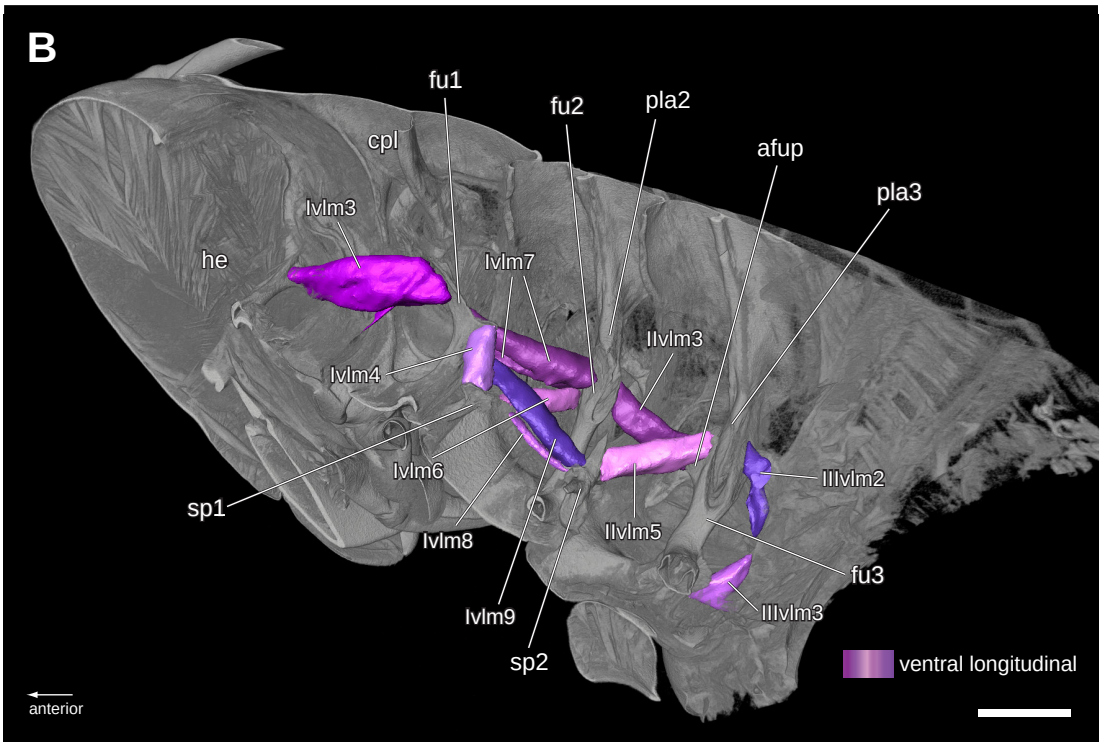

A
Idlm3
Idlm2
Idlm5
Idlm6
IIdlm1
IIdlm2
IIIdlm1
IIIdlm2
Idlm1
Idlm6
IIpcm5
IIIpcm5
Ipcm8
IIppm1
IIIppm1
pleuropleural
pleurocoxal
dorsal longitudinal
anterior
B
Ipcm4
IIpcm3
IIpcm4
Ipcm3
IIIpcm3
IIpcm1
IIIpcm4
IIpcm2
IIIpcm2
IIIpcm1
pleurocoxal
anterior



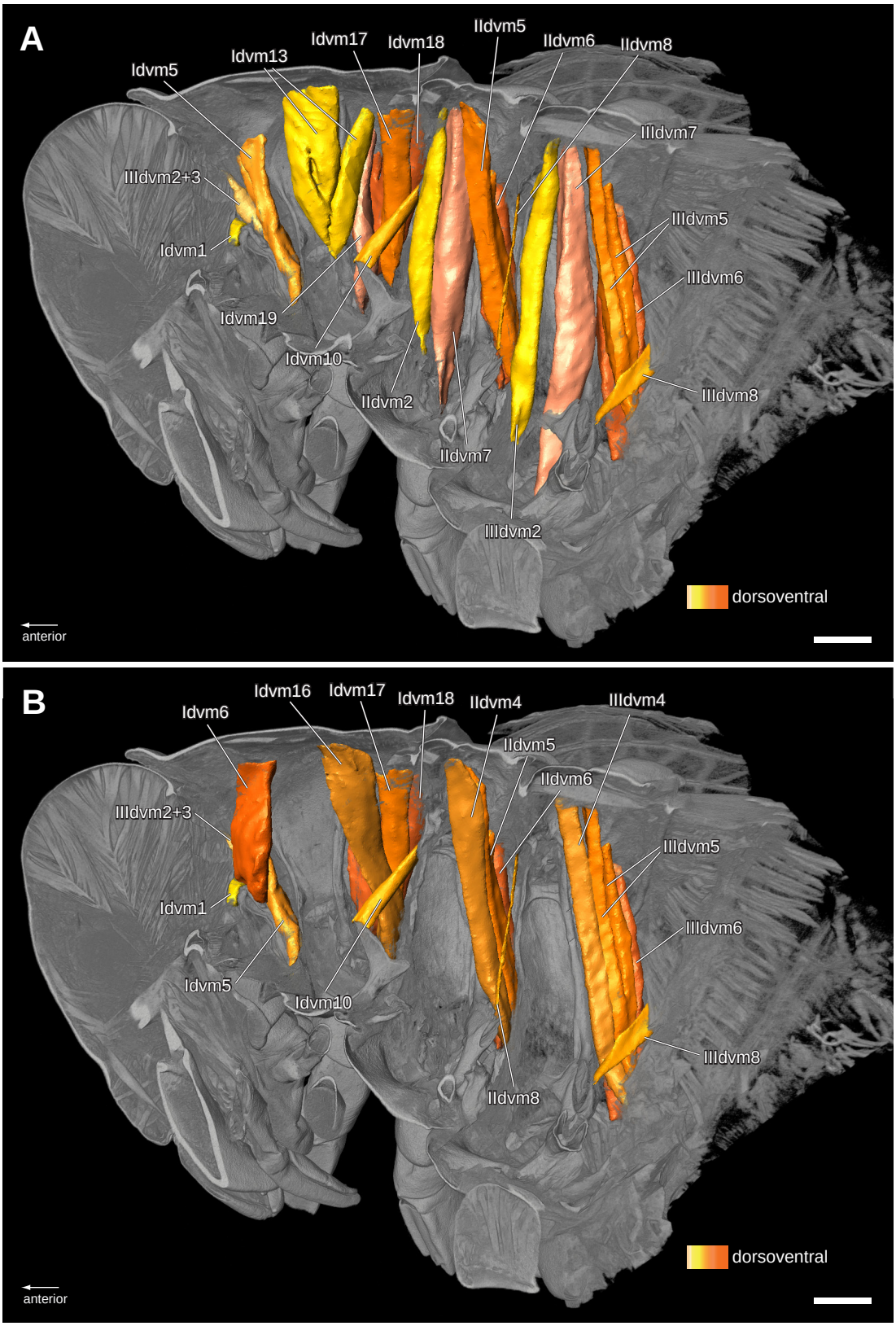
Supplementary Plate 27. Thoracic musculature of *Prosopogryllacris* sp. (Ensifera: Gryllacrididae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. Tergopleural muscles (tpm) of the pterothorax. Blue aterisks mark pleural ridge. Abbreviations: *em2/3* mes-/metepimeron, *est2/3* mes-/metepisternum, *fu1* profurca, *nt1/2/3* pro-/meso-/metanotum, *pla2* mesothoracic pleural arm. Scale bars: 1mm.

Supplementary Plate 28 (see opposite page). Thoracic musculature of *Prosopogryllacris* sp. (Ensifera: Gryllacrididae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Tergopleural muscles (tpm), sternopleural muscles (spm) and ventral longitudinal muscles (vlm). (B) Ventrolateral view. Upper body half clipped off. Ventral longitudinal muscles (vlm). Abbreviations: *afup* anterior furcal process, *cpl* cryptopleura, *fu1/2/3* pro-/meso-/metafurca, *he* head, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.

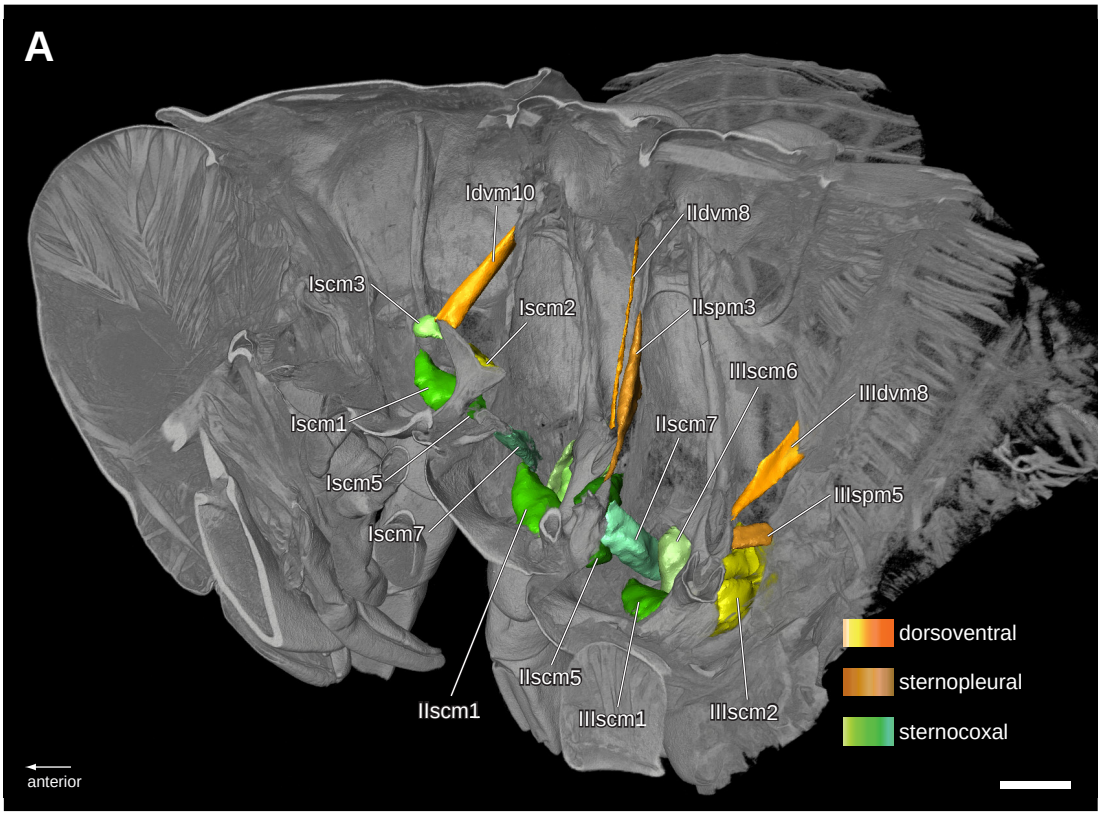

A
Iltpm9
Iltpm8
IIItpm1
Iltpm2
Iltpm1
IIItpm2
Ispm1
IIItpm9
Itpm2
IIItpm8
IIItpm10
IIspm2
Ivlm3
IIspm3
Ivlm4
IIvlm3
IIIspm2
IIIspm5
Ivlm7
IIIvlm2
tergopleural
sternopleural
Ivlm6
Ivlm8
IIvlm5
IIIvlm3
ventral longitudinal
anterior

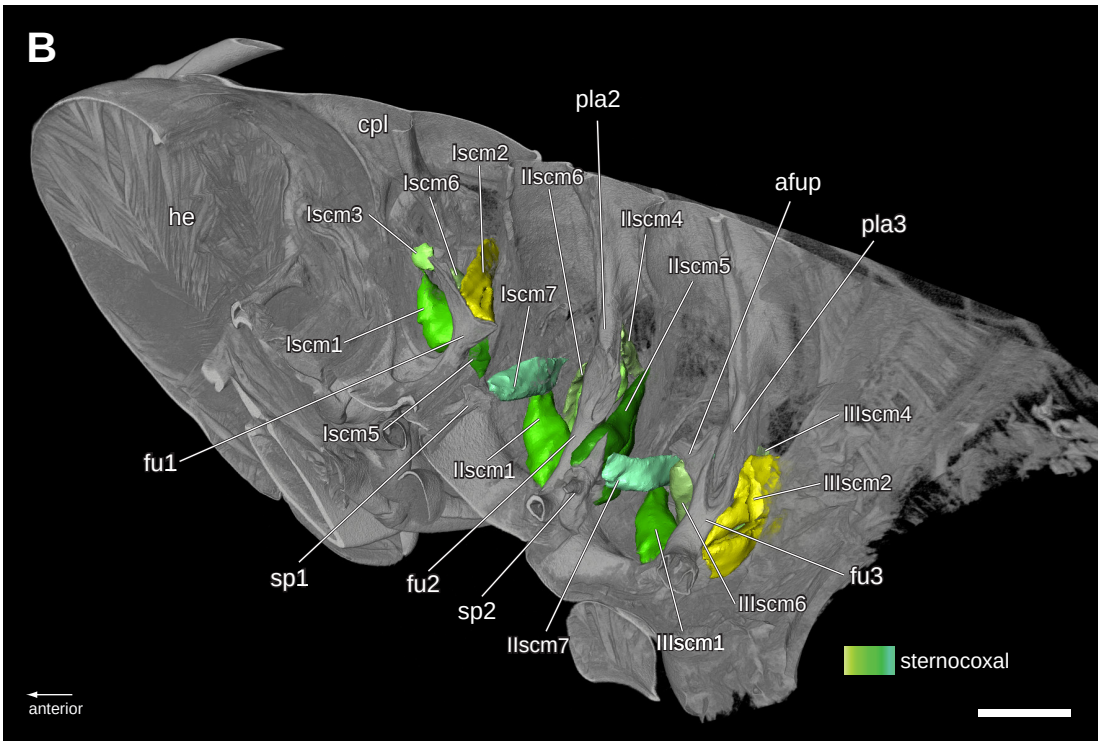

B
fu1
fu2
pla2
cpl
afup
pla3
Ivlm3
he
Ivlm7
IIvlm3
Ivlm4
Ivlm6
IIIvlm2
sp1
IIvlm5
Ivlm8
fu3
Ivlm9
IIIvlm3
sp2
ventral longitudinal
anterior

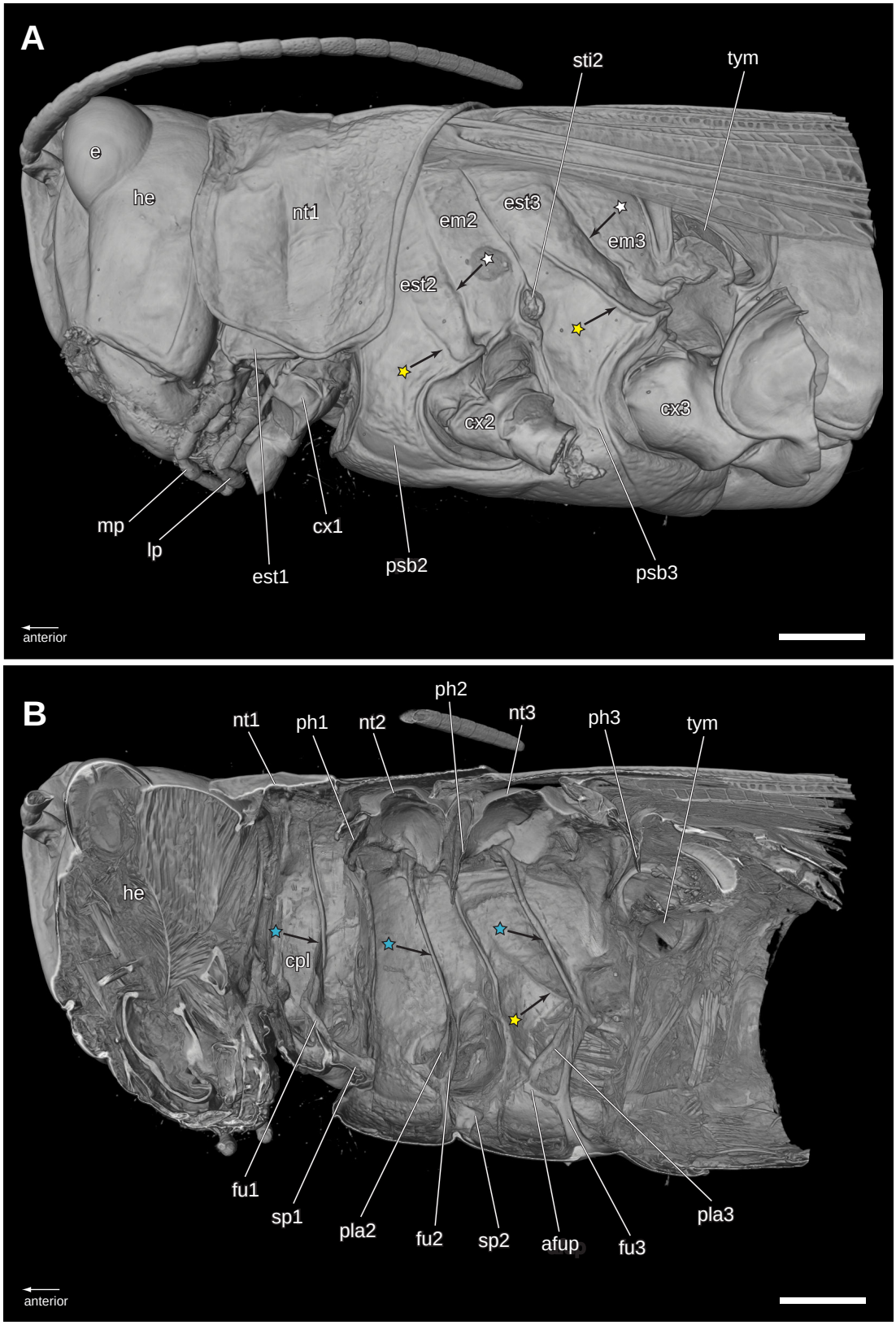
Supplementary Plate 29 (see opposite page). Thoracic musculature of *Prosopogryllacris* sp. (Ensifera: Gryllacrididae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. Dorsoventral musclus (dvm). (A)–(B) Virtual dissection. Scale bars: 1mm.

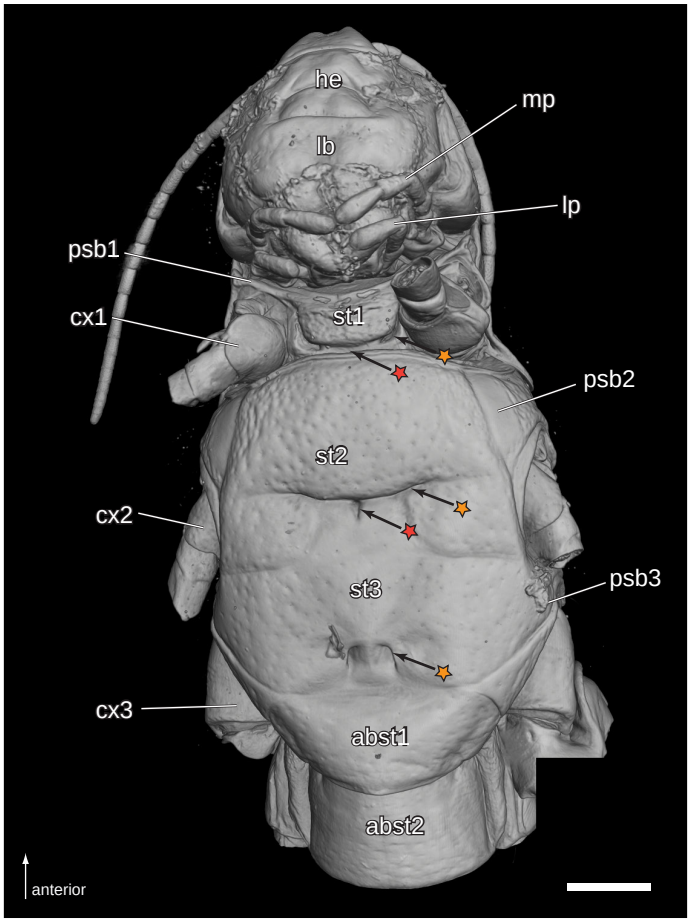

A
Idvm5
Idvm13
Idvm17
Idvm18
IIdvm5
IIdvm6
IIdvm8
IIIdvm7
IIIdvm2+3
IIIdvm5
Idvm1
IIIdvm6
Idvm19
Idvm10
IIdvm2
IIIdvm8
IIdvm7
IIIdvm2
dorsoventral
anterior
B
Idvm16
Idvm17
Idvm18
IIdvm4
IIIdvm4
Idvm6
IIdvm5
IIdvm6
IIIdvm2+3
IIIdvm5
Idvm1
IIIdvm6
Idvm5
Idvm10
IIIdvm8
IIdvm8
dorsoventral
anterior

Supplementary Plate 30 (see opposite page). Thoracic musculature of *Prosopogryllacris* sp. (Ensifera: Gryllacrididae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Dorsoventral muscles (dvm) (in part), sternopleural muscles (spm) (in part) and sternocoxal muscles (scm). (B) Ventrolateral view. Upper body half clipped off. Sternopleural muscles (vlm). Abbreviations: *afup* anterior furcal process, *cpl* cryptopleura, *fu1/2/3* pro-/meso-/metafurca, *he* head, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.


A
Idvm10
IIdvm8
Iscm3
Iscm2
IIspm3
IIIscm6
IIIdvm8
Iscm1
IIscm7
Iscm5
IIIspm5
Iscm7
dorsoventral
sternopleural
sternocoxal
IIscm5
IIscm1
IIIscm1
IIIscm2
anterior

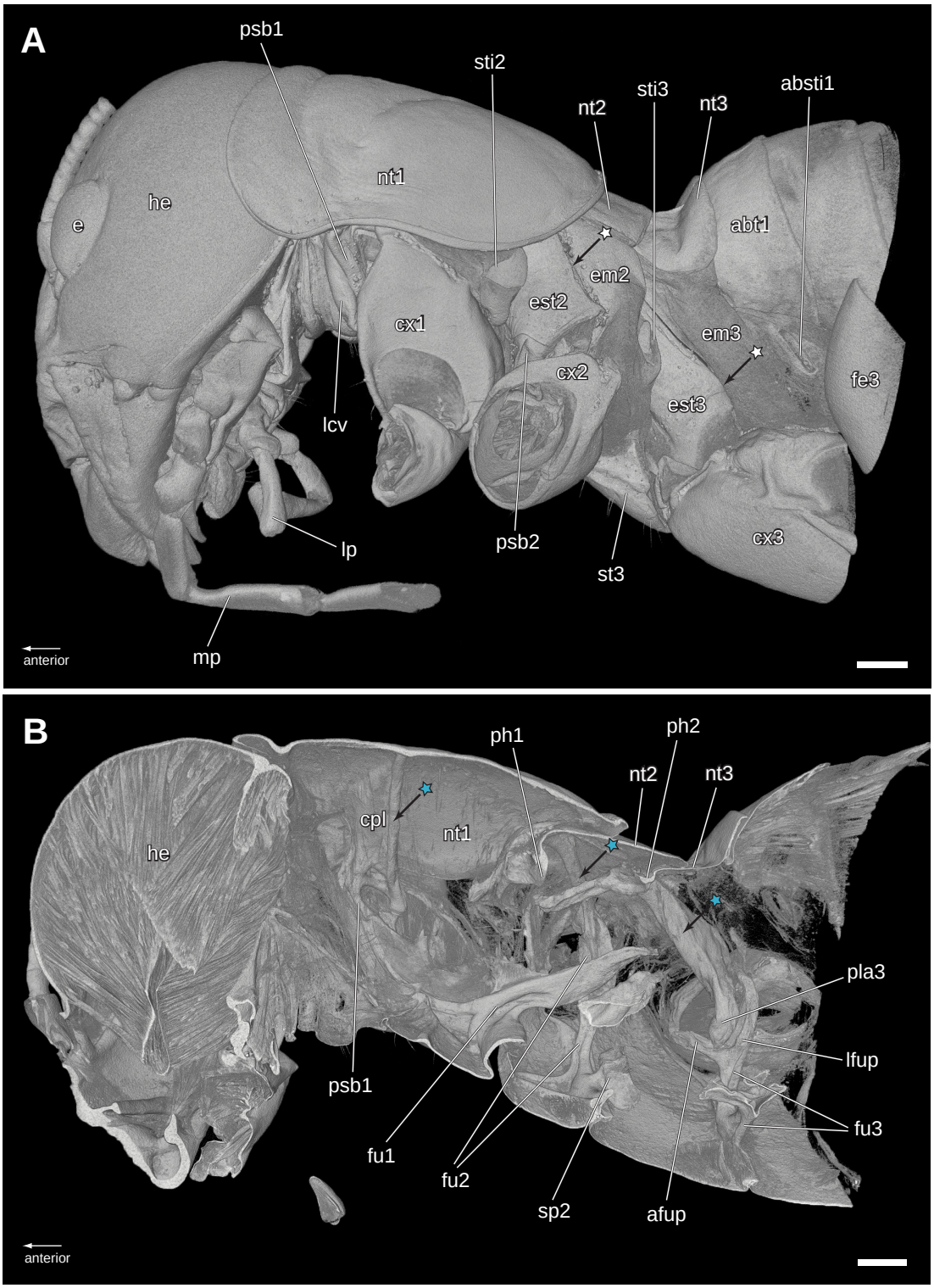

B
pla2
cpl
Iscm2
Iscm6
IIscm6
afup
he
Iscm3
IIscm4
pla3
IIscm5
Iscm7
Iscm1
IIIscm4
Iscm5
fu1
IIscm1
IIIscm2
fu3
sp1
fu2
sp2
IIIscm6
IIscm7
IIIscm1
sternocoxal
anterior

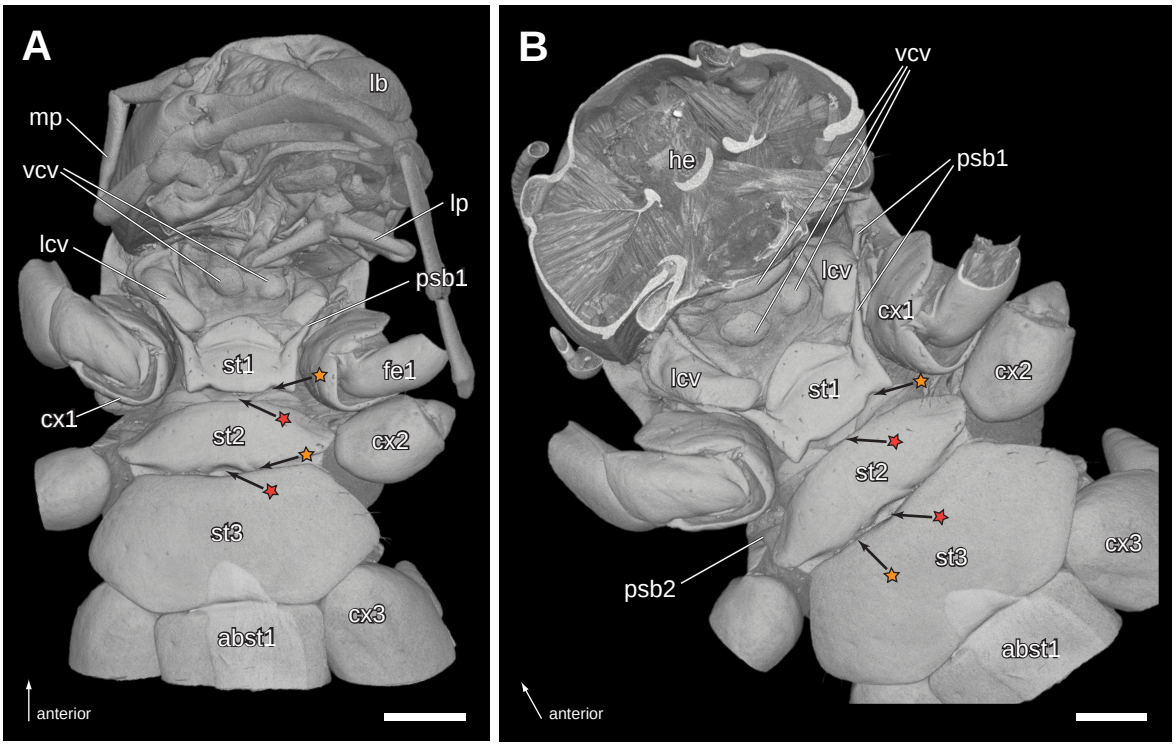

A
sti2
tym
e
he
nt1
em2
est3
em3
est2
cx2
cx3
mp
lp
cx1
est1
psb2
psb3
anterior
B
ph2
nt1
ph1
nt2
nt3
ph3
tym
he
cpl
fu1
sp1
pla2
fu2
sp2
afup
fu3
pla3
anterior



Supplementary Plate 31. Thoracic skeleton of *Stenobothrus lineatus* (Caelifera: Acrididae). Female. Three-dimensional volume rendering based on µCT-sections. Exterior ventral view. Orange asterisks mark invagination points of pro- and metafurca. Furcal pit of mesofurca hidden by mesosternum. Red asterisks mark invagination points of pro- and mesospina. Abbreviations: *abst1/2* first/second abdominal sternum, *cx1/2/3* pro-/meso-/metacoxa, *he* head, *lb* labrum, *lp* labial palp, *mp* maxillary palp, *psb1/2/3* pro-/meso-/metathoracic pleurosternal bridge, *st1/2/3* pro-/meso-/metasternum. Scale bars: 1mm.

Supplementary Plate 32 (see opposite page). Thoracic skeleton of *Stenobothrus lineatus* (Caelifera: Acrididae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Yellow asterisks mark strongly sclerotized ridge betwwen episternum and its anterior margin. Blue asterisks mark pleural ridge. Abbreviations: *afup* anterior furcal process, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *em2/3* mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *ph1/2/3* pro-/meso-/metaphragma, *pla2/3* meso-/metathoracic pleural arm, *psb2/3* meso-/metathoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *sti2* mesothoracic stigma, *tym* tympanal rgan on first abdominal segment. Scale bars: 1mm.

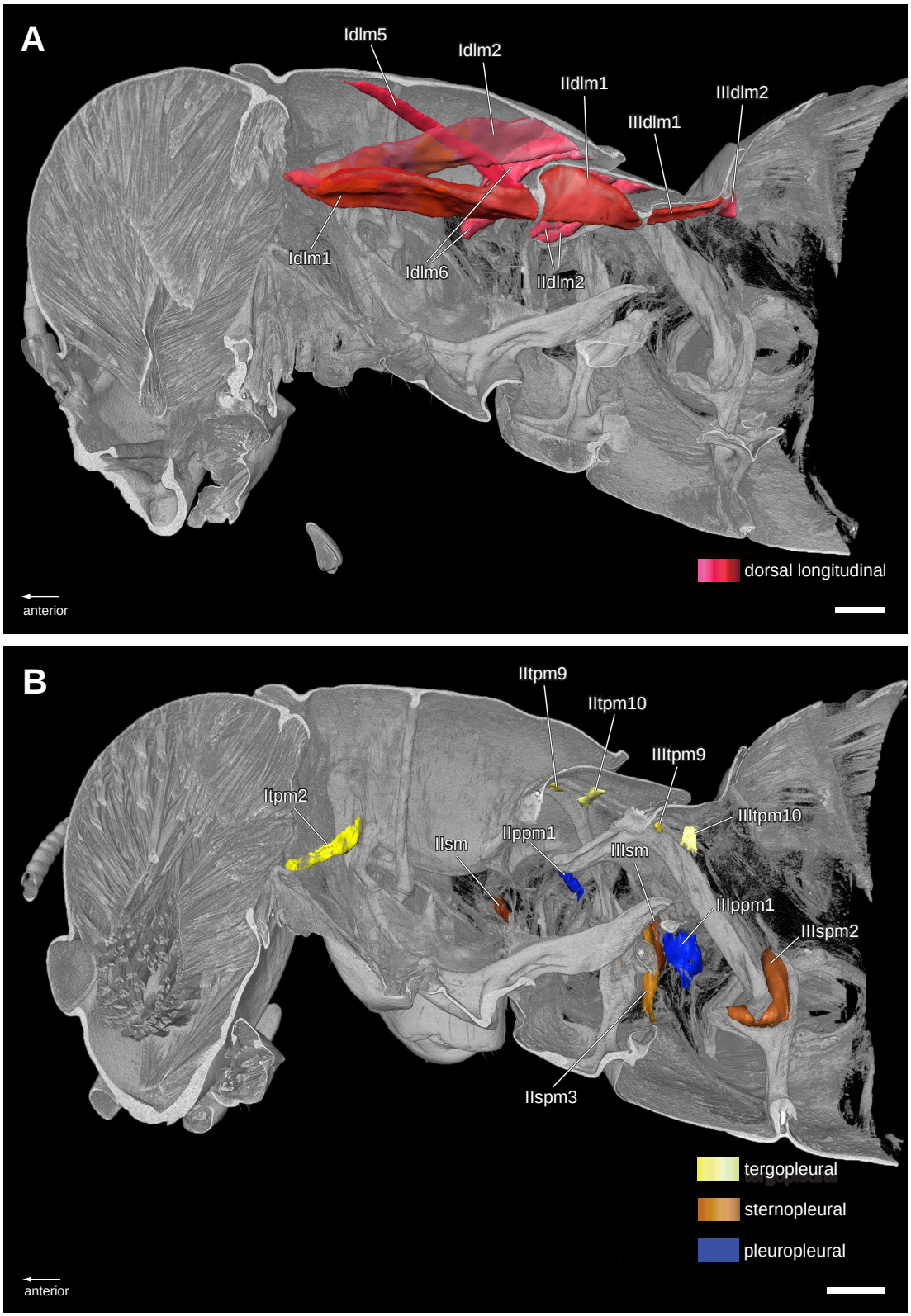

A
psb1
sti2
sti3
nt2
nt3
absti1
nt1
he
e
abt1
em2
est2
cx1
em3
cx2
fe3
est3
lcv
lp
psb2
st3
cx3
mp
anterior
B
ph1
ph2
nt2
nt3
cpl
nt1
he
pla3
lfup
psb1
fu3
fu1
fu2
sp2
afup
anterior



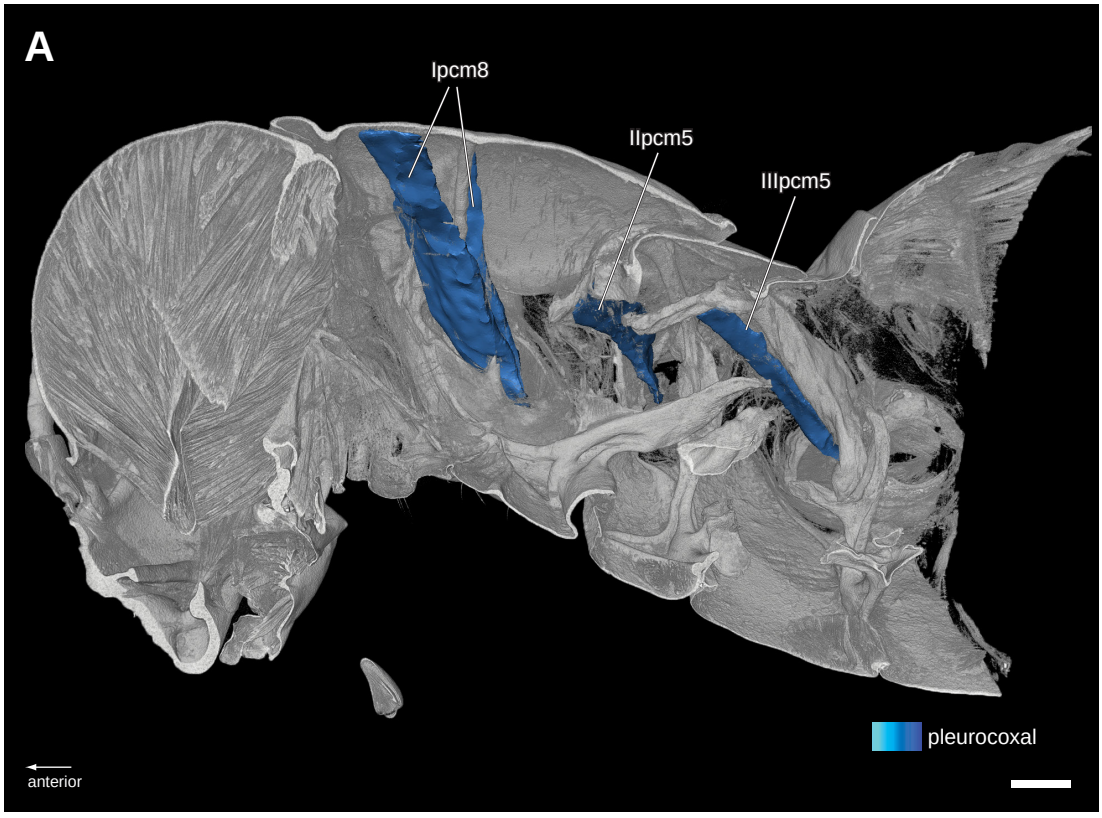
Supplementary Plate 33. Thoracic skeleton of *Stenopelmatus* sp. (Ensifera: Stenopelmatidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior ventral view. (B) Shifted ventral view. Head and mouthparts clipped off to show ventral cervical region. Orange asterisks mark invagination points of pro- and metafurca. Red asterisks mark invagination points of pro- and mesospina. Abbreviations: *abst1/2* first/second abdominal sternum, *cx1/2/3* pro-/meso-/metacoxa, *he* head, *lb* labrum, *lcv* lateral cervical sclerite, *lp* labial palp, *mp* maxillary palp, *psb1/2* pro-/mesothoracic pleurosternal bridge, *st1/2/3* pro-/meso-/metasternum, *vcv* ventral cervical sclerite. Scale bars: 1mm.

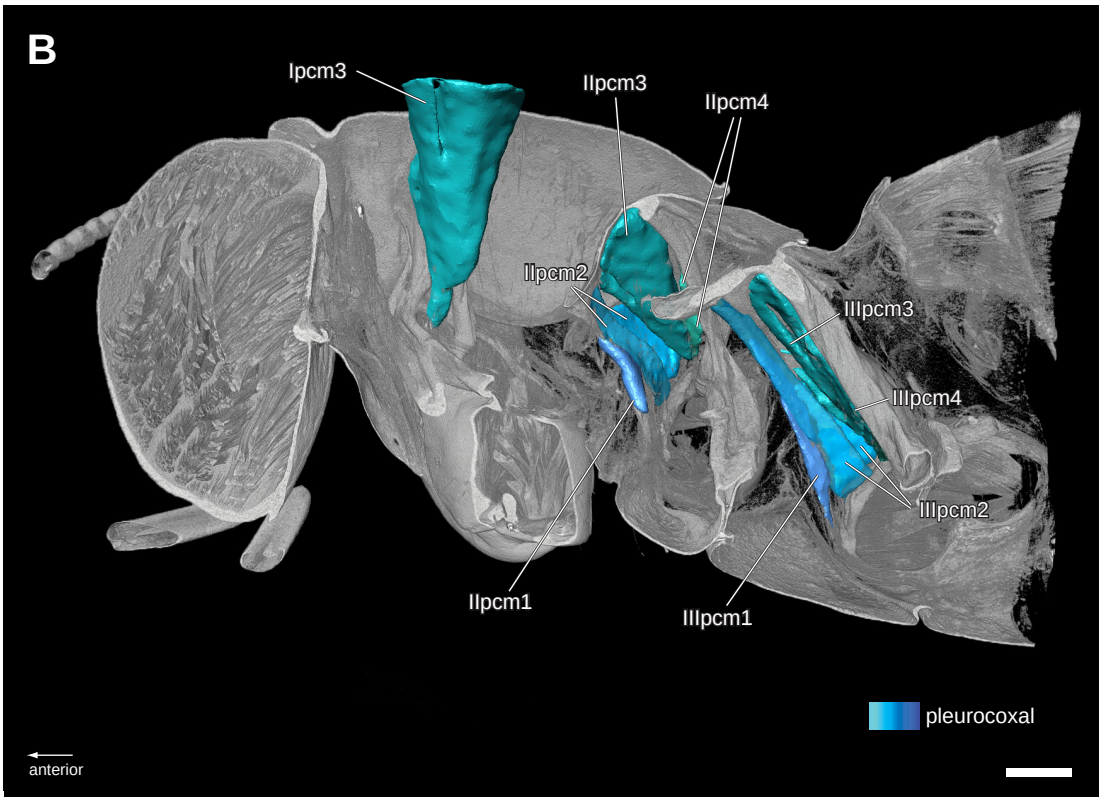
Supplementary Plate 34 (see opposite page). Thoracic skeleton of *Stenopelmatus* sp. (Ensifera: Stenopelmatidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. White asterisks mark pleural suture. Blue asterisks mark pleural ridge. Abbreviations: *absti1* first abdominal stigma, *abt1* first abdominal tergum, *afup* anterior furcal process, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *em2/3* mes-/metepimeron, *est2/3* mes-/metepisternum, *fe3* metafemur, *fu1/2/3* pro-/meso-/metafurca, *he* head, *lcv* lateral cervical sclerite, *lfup* lateral furcal process, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *ph1/2* pro-/mesophragma, *pla2/3* meso-/metathoracic pleural arm, *psb1/2* pro-/mesothoracic pleurosternal bridge, *sp1/2* pro-/mesospina, *st3* metasternum, *sti2/3* meso-/metathoracic stigma. Scale bars: 1mm.

Supplementary Plate 35 (see opposite page). Thoracic musculature of *Stenopelmatus* sp. (Ensifera: Stenopelmatidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Midsagittal cut. Dorsal longitudinal muscles (dlm). (B) Sagittal cut. Tergopleural muscles (tpm), sternopleural muscles (spm) and pleuropleural muscles (ppm). Short stigmatic muscles (II/IIsm) also illustrated. Scale bars: 1mm.

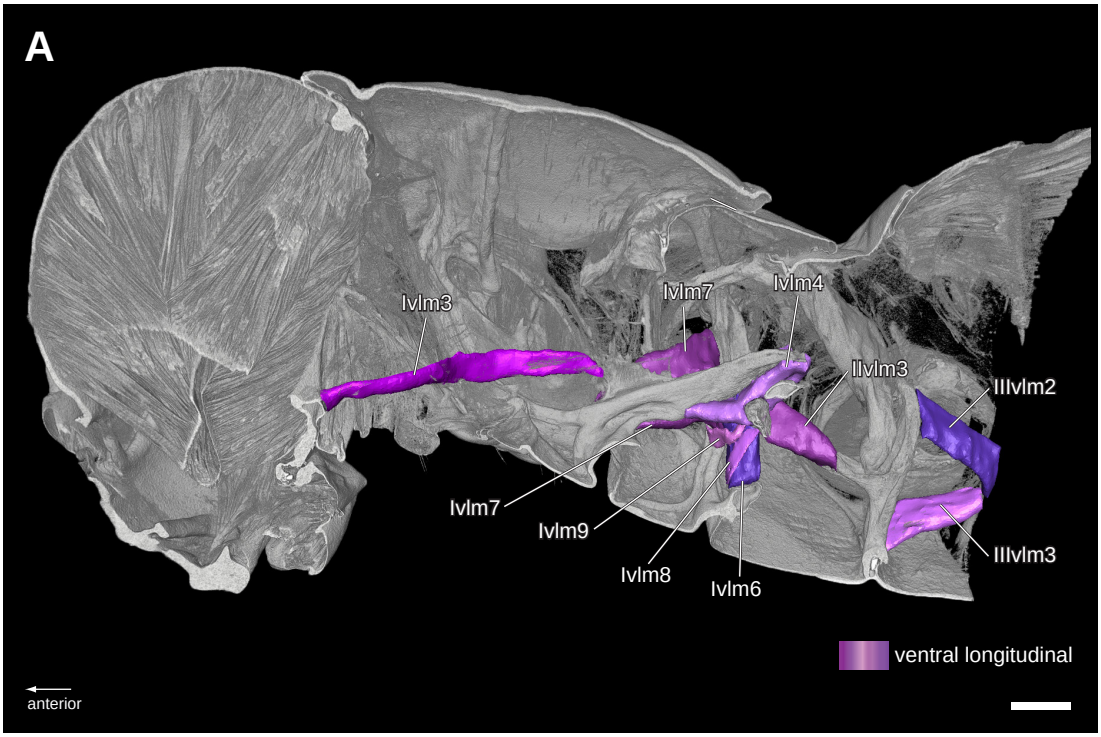

A
Idlm5
Idlm2
IIdlm1
IIIdlm2
IIIdlm1
Idlm1
Idlm6
IIdlm2
dorsal longitudinal
anterior
B
IItpm9
IItpm10
IIItpm9
Itpm2
IIIItpm10
IIppm1
IIsm
IIIsm
IIIppm1
IIIspm2
IIspm3
tergopleural
sternopleural
pleuropleural
anterior

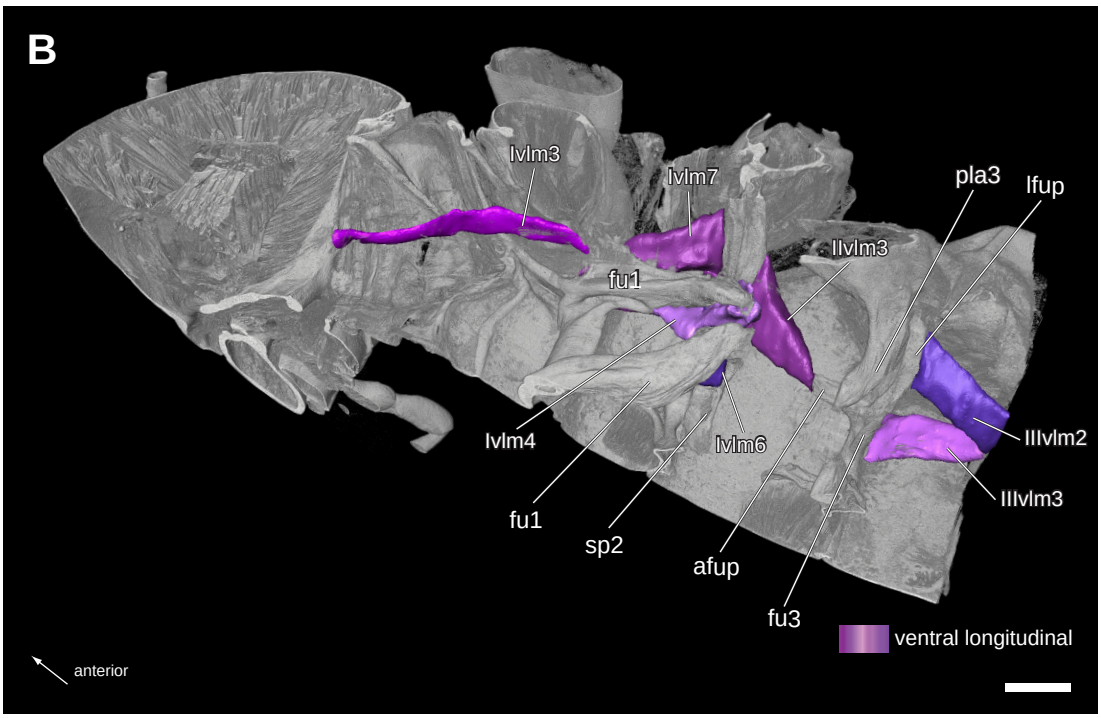
Supplementary Plate 36 (see opposite page). Thoracic musculature of *Stenopelmatus* sp. (Ensifera: Stenopelmatidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. (A) Midsagittal cut. Pleurocoxal muscles (pcm) (in part). (B) Sagittal cut. Pleurocoxal muscles (pcm) (in part). Scale bars: 1mm.


A
Ipcm8
IIpcm5
IIIpcm5
pleurocoxal
anterior

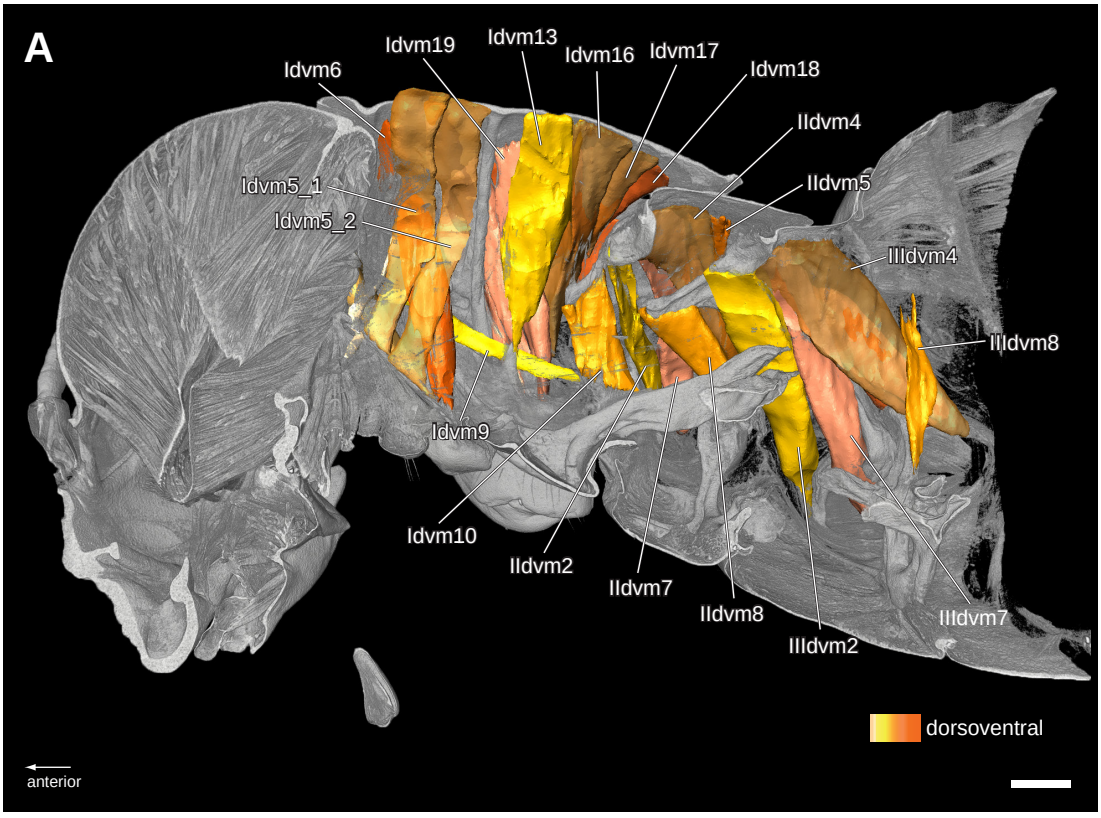

B
Ipcm3
IIpcm3
IIpcm4
IIpcm2
IIIpcm3
IIIpcm4
IIIpcm2
IIpcm1
IIIpcm1
pleurocoxal
anterior

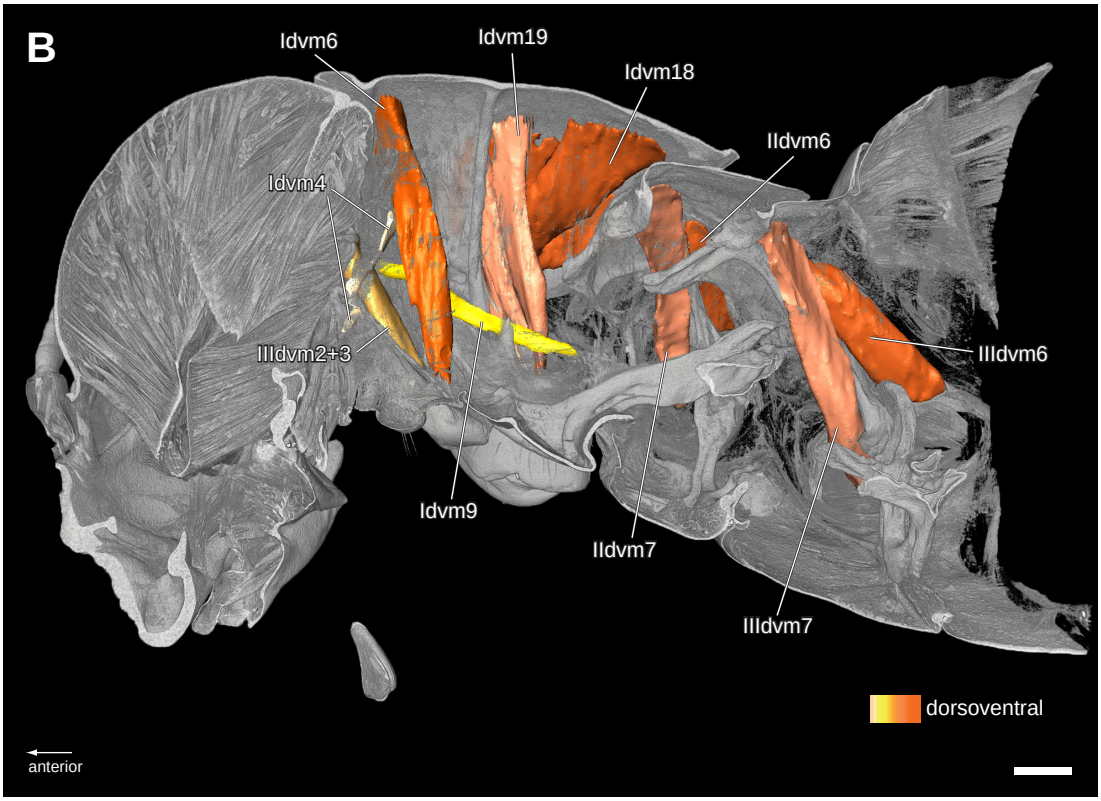
Supplementary Plate 37 (see opposite page). Thoracic musculature of *Stenopelmatus* sp. (Ensifera: Stenopelmatidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Ventral longitudinal muscles (vlm). IIvlm5 not illustrated. (A) Interior lateral view. (B) Ventrolateral view. Upper body half clipped off. Abbreviations: *afup* anterior furcal process, *fu1/2/3* pro-/meso-/metafurca, *lfup* lateral furcal process, *pla3* metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.


A
lvlm3
lvlm7
lvlm4
IIlvlm3
IIIvlm2
lvlm7
lvlm9
lvlm8
lvlm6
IIIvlm3
ventral longitudinal
anterior

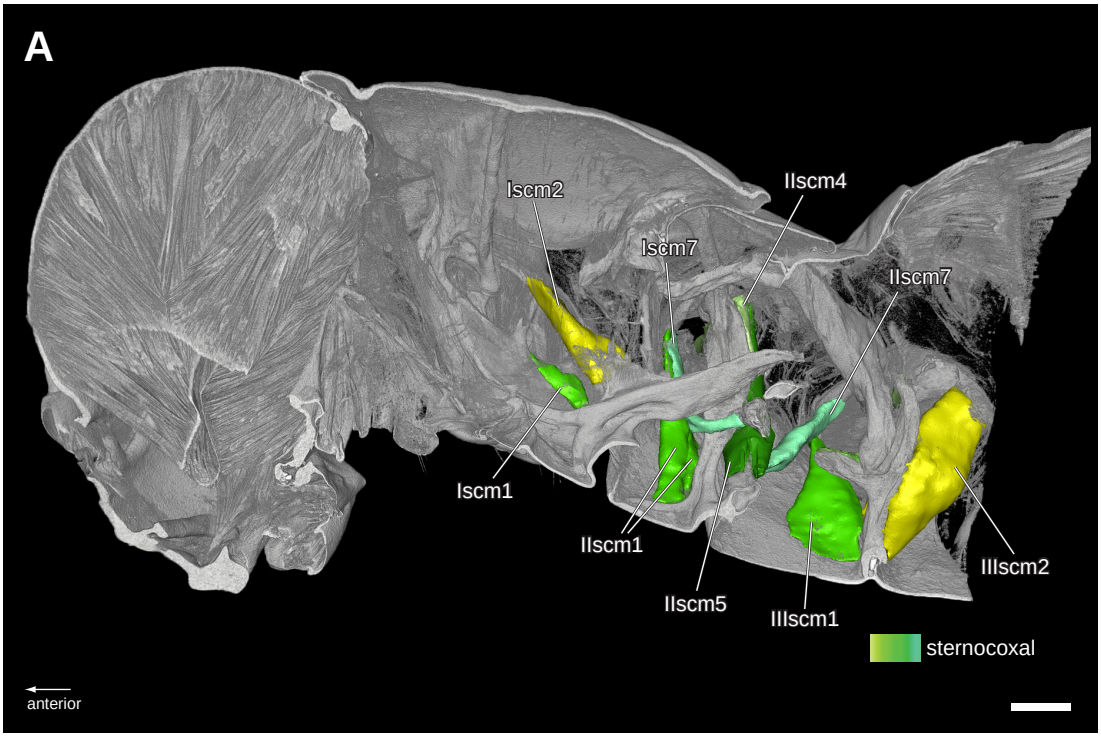

B
lvlm3
lvlm7
pla3
lfup
IIlvlm3
fu1
lvlm4
lvlm6
IIIvlm2
IIIvlm3
fu1
sp2
afup
fu3
ventral longitudinal
anterior

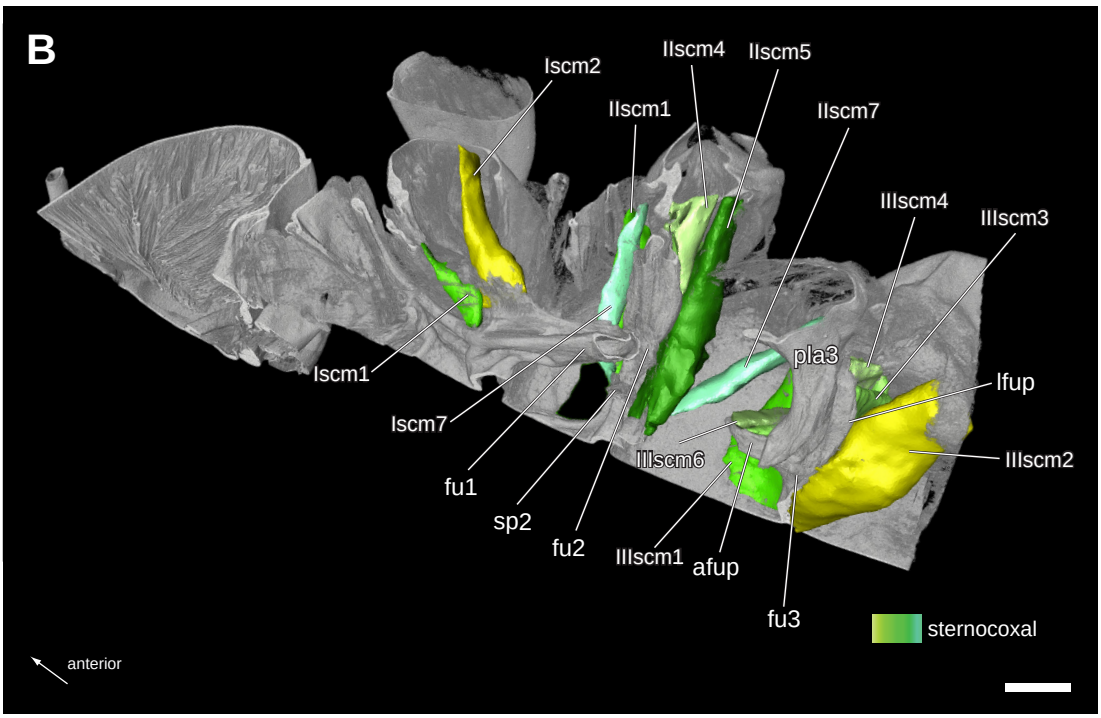
Supplementary Plate 38 (see opposite page). Thoracic musculature of *Stenopelmatus* sp. (Ensifera: Stenopelmatidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. Dorsoventral muscles (dvm). (A)−(B) Virtual dissection. Scale bars: 1mm.

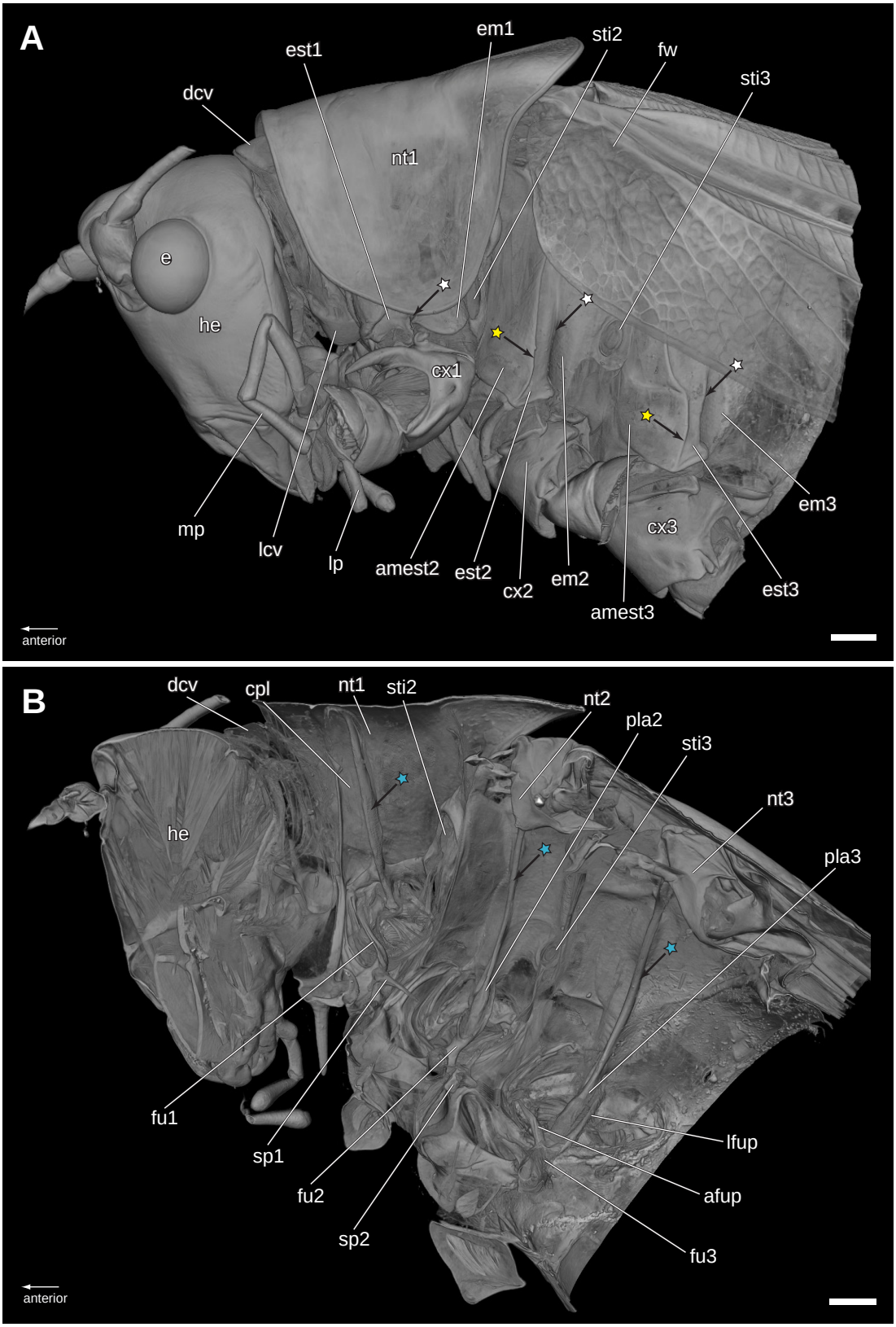

A
ldvm6
ldvm19
ldvm13
ldvm16
ldvm17
ldvm18
lldvm4
ldvm5_1
ldvm5_2
lldvm5
IIIdvm4
IIIdvm8
ldvm9
ldvm10
lldvm2
lldvm7
lldvm8
IIIdvm2
IIIdvm7
dorsoventral
anterior

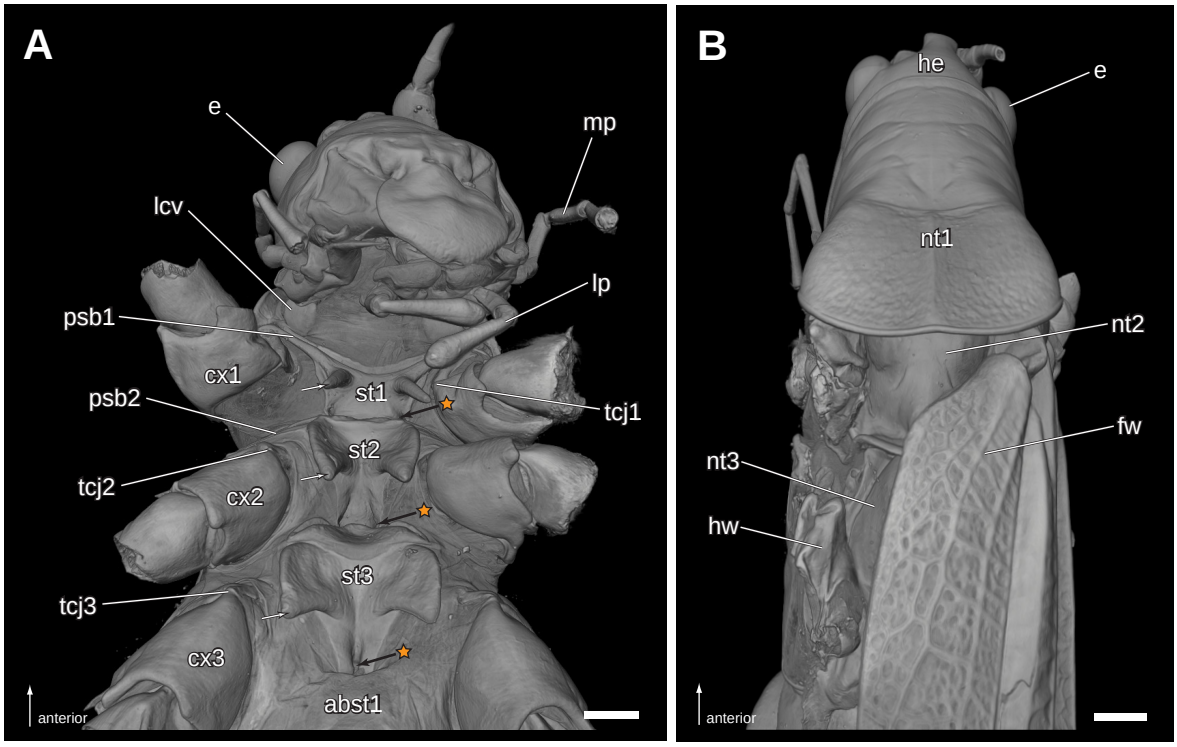

B
ldvm6
ldvm19
ldvm18
lldvm6
ldvm4
IIIdvm2+3
IIIdvm6
ldvm9
lldvm7
IIIdvm7
dorsoventral
anterior

Supplementary Plate 39 (see opposite page). Thoracic musculature of *Stenopelmatus* sp. (Ensifera: Stenopelmatidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Sternocoxal muscles (scm). (A) Interior lateral view. (B) Ventrolateral view. Upper body half clipped off. Abbreviations: *afup* anterior furcal process, *fu1/2/3* pro-/meso-/metafurca, *lfup* lateral furcal process, *pla3* metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.


A
Iscm2
IIscm4
Iscm7
IIscm7
Iscm1
IIscm1
IIscm5
IIIscm1
IIIscm2
sternocoxal
anterior

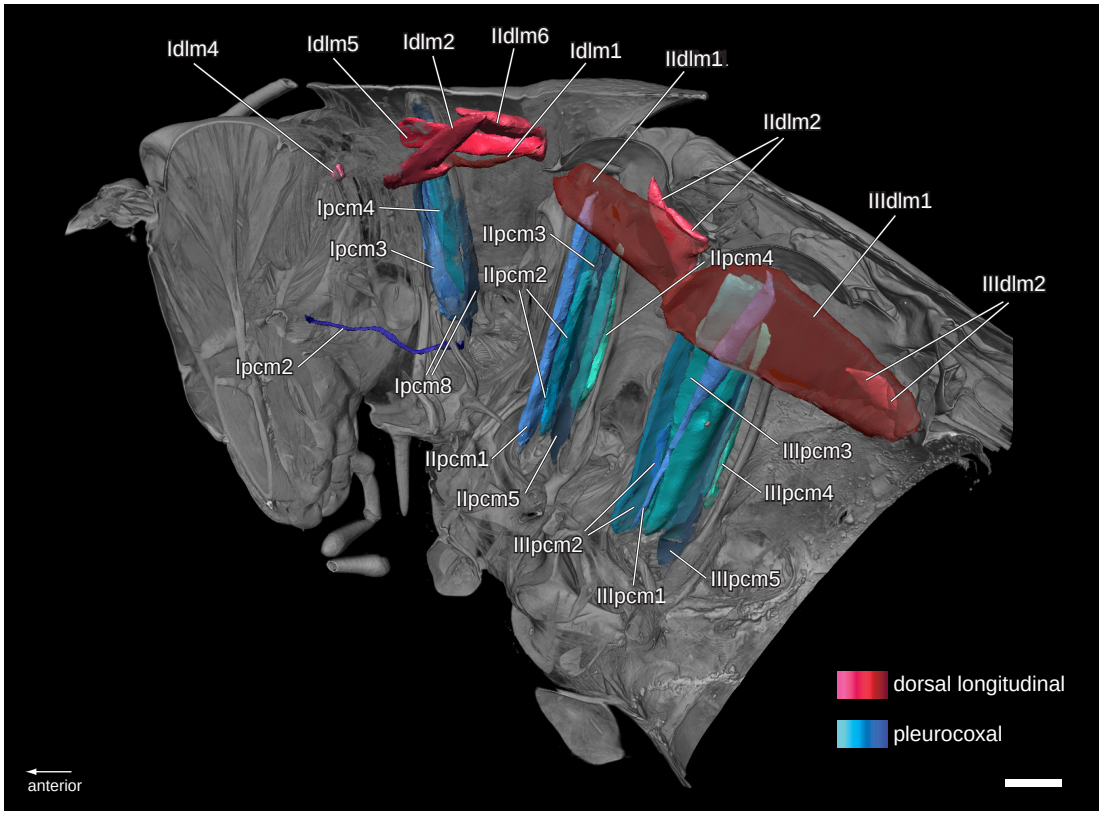

B
Iscm2
IIscm4
IIscm5
IIscm1
IIscm7
IIIscm4
IIIscm3
pla3
Iscm1
Iscm7
lfup
IIIscm6
IIIscm2
fu1
sp2
fu2
IIIscm1
afup
fu3
sternocoxal
anterior


A
em1
sti2
fw
est1
sti3
dcv
nt1
e
he
cx1
em3
mp
lcv
lp
amest2
est2
cx2
em2
cx3
amest3
est3
anterior
B
dcv
cpl
nt1
sti2
nt2
pla2
sti3
nt3
he
pla3
fu1
sp1
fu2
sp2
lfup
afup
fu3
anterior



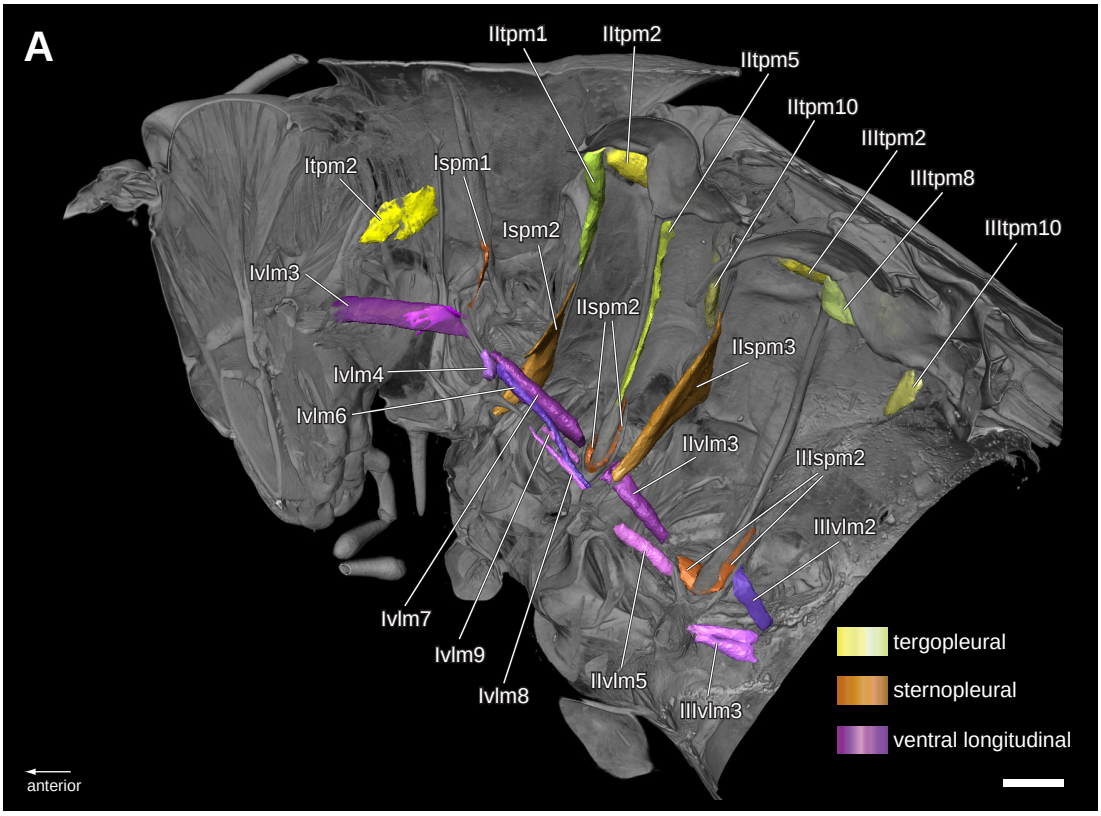
Supplementary Plate 40. Thoracic skeleton of *Tettigonia viridissima* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior ventral view. White arrows mark sternal spines on pro-/meso-/metasternum. Orange asterisks mark invagination points of pro- and metafurca. Invagination points of pro- and mesospina not visible from this point of view. (B) Exterior dorsal view. Wings of left body side removed, only wing basis of hindwing (*hw*) remained. Abbreviations: *abst1/2* first/second abdominal sternum, *cx1/2/3* pro-/meso-/metacoxa, *e* compound eye, *fw* forewing, *he* head, *hw* hindwing, *lb* labrum, *lcv* lateral cervical sclerite, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *psb1/2* pro-/mesothoracic pleurosternal bridge, *st1/2/3* pro-/meso-/metasternum, *tcj1/2/3* pro-/meso-/metathoracic trochantino-coxal joint, *vcv* ventral cervical sclerite. Scale bars: 1mm.

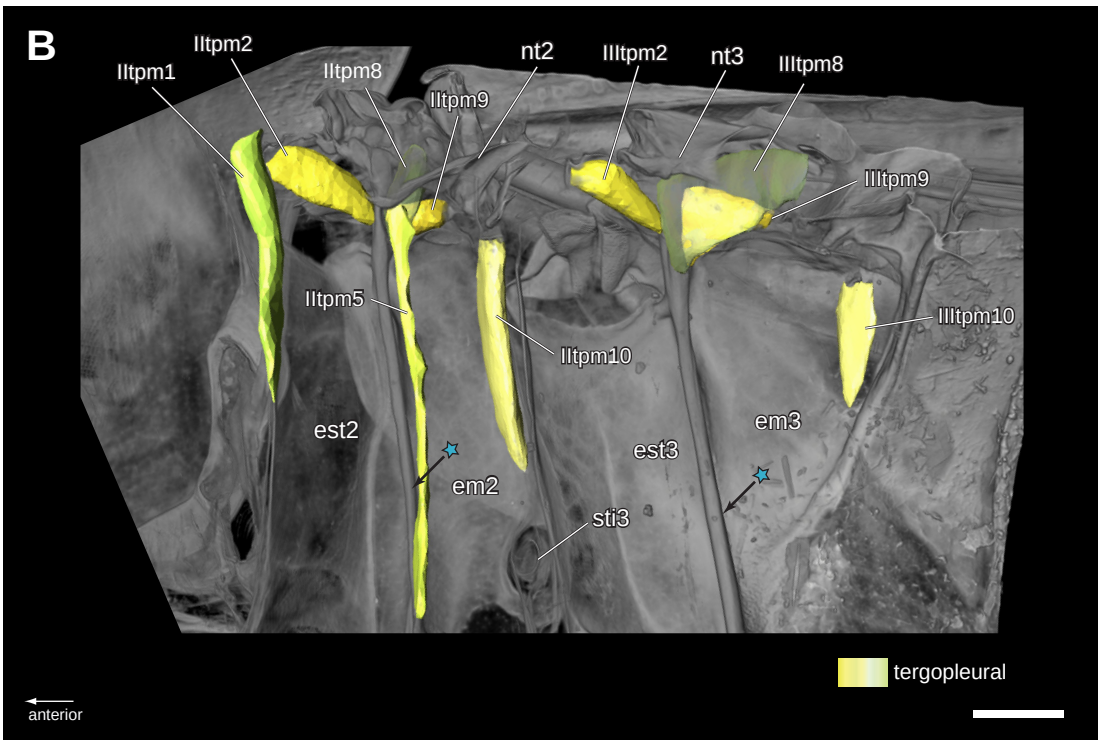
Supplementary Plate 41 (see opposite page). Thoracic skeleton of *Tettigonia viridissima* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. (A) Exterior lateral view. (B) Interior lateral view. Phragmata not visible in cutting plane. White asterisks mark pleural suture. Yellow asterisks mark strongly slerotized ridge between episternum and its anterior margin. Blue asterisks mark pleural ridge. Abbreviations: *afup* anterior furcal process, *amest2/3* anterior margin of mes-/metepisternum, *cpl* cryptopleura, *cx1/2/3* pro-/meso-/metacoxa, *dcv* dorsal cervical sclerite, *e* compound eye, *em1/2/3* pro-/mes-/metepimeron, *est1/2/3* pro-/mes-/metepisternum, *fu1/2/3* pro-/meso-/metafurca, *fw* forewing, *he* head, *lcv* lateral cervical sclerite, *lfup* lateral furcal process, *lp* labial palp, *mp* maxillary palp, *nt1/2/3* pro-/meso-/metanotum, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina, *sti2/3* meso-/metathoracic stigma. Scale bars: 1mm.

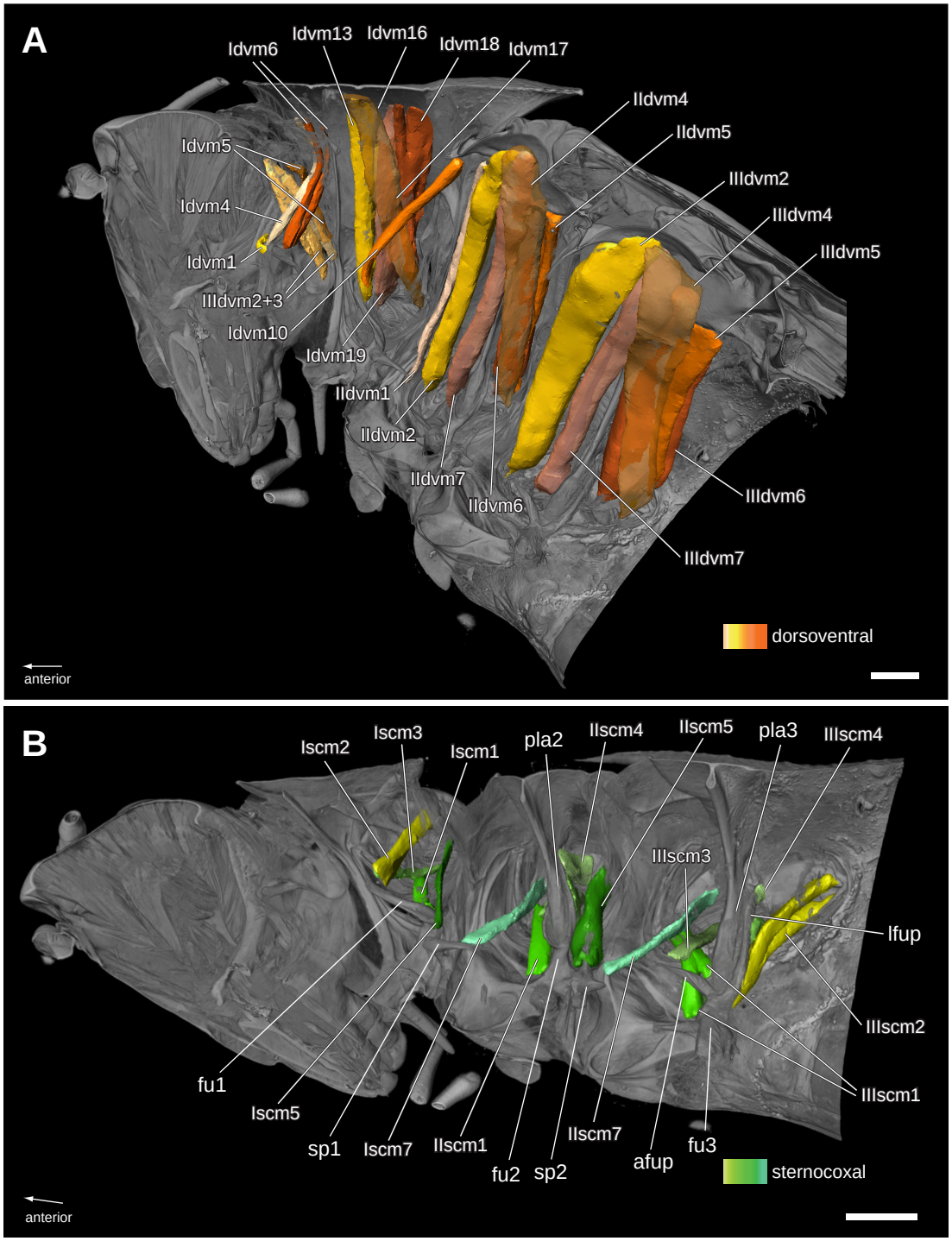


Supplementary Plate 42. Thoracic musculature of *Tettigonia viridissima* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Interior lateral view. Dorsal longitudinal muscles (dlm) and pleurocoxal muscles (pcm). Scale bars: 1mm.

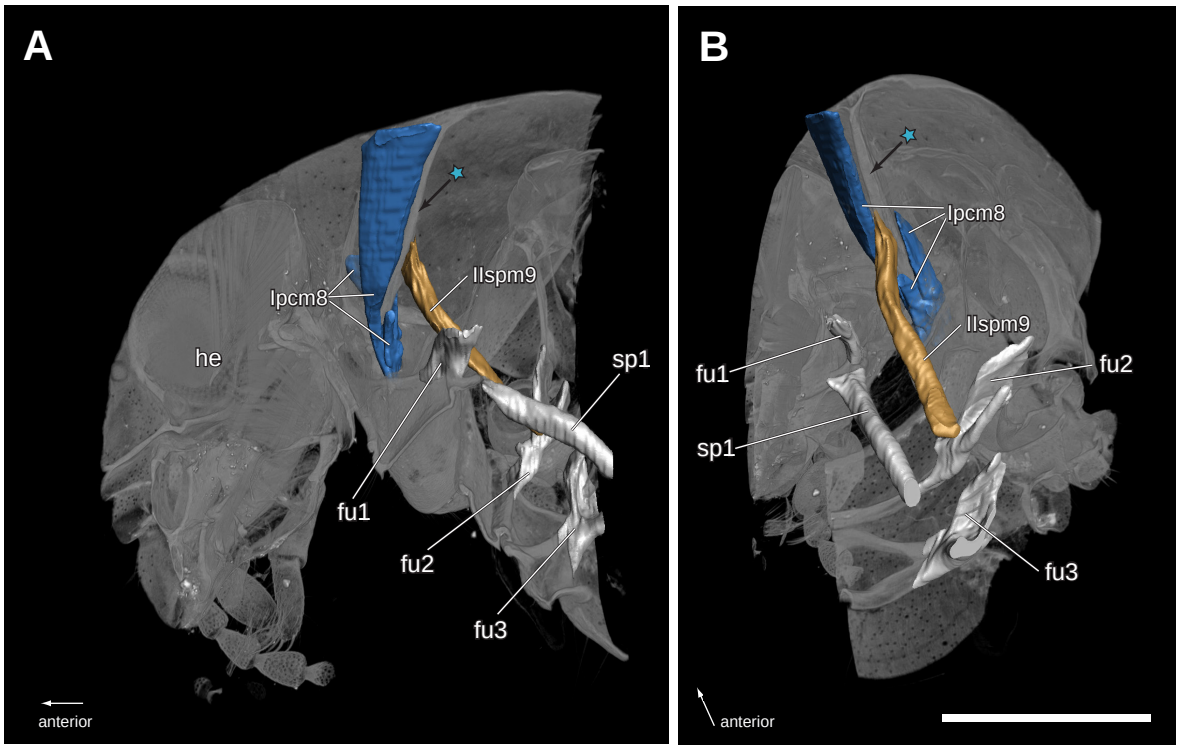
Supplementary Plate 43 (see opposite page). Thoracic musculature of *Tettigonia viridissima* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. (A) Interior lateral view. Tergopleural muscles (tpm), sternopleural muscles (spm) and ventral longitudinal muscles (vlm). (B) Slightly shifted dorsolateral view of pterothorax. Tergopleural muscles (tpm) of pterothorax. Blue asterisks mark pleural ridge. Abbreviations: *em2/3* pro-/mes-/metepimeron, *est2/3* pro-/mes-/metepisternum, *sti3* mesothracic stigma. Scale bars: 1mm.


A
Iltpm1
Iltpm2
Iltpm5
Iltpm10
IIItpm2
IIItpm8
IIItpm10
Itpm2
Ispm1
Ispm2
Ivlm3
IIspm2
IIspm3
Ivlm4
Ivlm6
IIvlm3
IIIspm2
IIIvlm2
Ivlm7
Ivlm9
Ivlm8
IIvlm5
IIIvlm3
tergopleural
sternopleural
ventral longitudinal
anterior


B
Iltpm1
Iltpm2
Iltpm8
Iltpm9
nt2
IIItpm2
nt3
IIItpm8
IIItpm9
Iltpm5
Iltpm10
IIItpm10
est2
em2
sti3
est3
em3
tergopleural
anterior



Supplementary Plate 44. Thoracic musculature of *Tettigonia viridissima* (Ensifera: Tettigoniidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. (A) Interior lateral view. Dorsoventral muscles (dvm). (B) Ventrolateral view. Upper body half clipped off. Sternocoxal muscles (scm). Abbreviations: *afup* anterior furcal process, *fu1/2/3* pro-/meso-/metafurca, *lfup* lateral furcal process, *pla2/3* meso-/metathoracic pleural arm, *sp1/2* pro-/mesospina. Scale bars: 1mm.



Supplementary Plate 45. Thoracic musculature of *Xya* sp. (Caelifera: Tridactylidae). Female. Three-dimensional volume rendering based on µCT-sections. Right body half. Sternal apophyses reconstructed in light grey. Course of Ipcm8 (M. propleuro-trohantinalis) and IIspm9 (M. mesofurca-propleuralis) illustrated. Blue asterisk marks pleural ridge of cryptopleura. (A) Interior lateral view. (B) Interior posterodorsal view. Abbreviations: *fu1/2/3* pro-/meso-/metafurca, *he* head, *sp1* prospina. Scale bar: 1mm.

General Discussion

Morphology of the skeletomuscular system in the thorax of Orthoptera

A number of studies on various parts of the thoracic skeletomuscular system of Orthoptera already exist, but exhaustive documentations were hitherto mainly based on exemplary anatomical studies of few model organisms, e.g. the house cricket *Acheta domesticus* (Voss 1905a,b) and some grasshopper species (Snodgrass 1929; Albrecht 1953; de Zolessi 1968). Most of these studies either give only a scarce or incomplete description of the thoracic skeleton or merely include a part of the thoracic musculature (e.g. Carpentier 1921, 1936; Maskell 1927; Gurney 1935; Richards 1955; Khattar & Srivastava 1962). To overcome this fragmentary knowledge on the morphology of the thorax in Orthoptera, one major aim of this thesis was to provide a comprehensive and detailed documentation of this character complex in representatives of all major ensiferan lineages. By including yet unstudied taxa such as Gryllacrididae and Stenopelmatidae, the herein presented studies represent the most comprehensive comparative investigation of the morphology of the thoracic skeletomuscular system of Orthoptera so far. Moreover, the obtained data set is used to reconstruct the orthopteran groundpattern of the thoracic skeleton and musculature (Chapter 3). Previously Wipfler *et al.* (2015) recovered a few obvious apomorphic characters of Orthoptera, e.g. the saddle-shaped pronotum and cryptopleura. The phylogenetic analysis of novel thoracic characters (Chapter 3) has yielded numerous additional apomorphies: the connection of propleura and prosternum as pleurosternal bridge (convergently evolved in praying mantises), the pterothoracic furcae that enclose the respective pleural arm from the ventral side, the mesofurca and mesospina that are situated in one line at the sternacosta, and a stalked mesospina with a delimited dorsal plate. In particular, the morphology of the sterna turned out to show major differences between both subgroups of Orthoptera, for instance the profurca that bears a single arm in Caelifera is branched in Ensifera (Chapter 3). The nomenclature of the thoracic muscles in Neoptera presented by Friedrich & Beutel (2008) served as a solid basis for the homologization of the thoracic musculature in Orthoptera. Hence, to a large extent the identification of muscles had been considerably evident, although the mere definition of muscles due to their origin and insertion appeared to make their homologization difficult in a few cases, e.g. to decide whether muscular points of origin or insertion are translocated to other thoracic

sclerites (Chapter 1). In this thesis, orthopteran-specific muscles are identified that have not been described before. Subsequently, these newly described thoracic muscles are named and defined according to the nomenclature of Friedrich & Beutel (2008) to provide comparability for future studies on the thoracic musculature of other neopteran insects.

Secondary winglessness in Ensifera and other polyneopteran lineages

The flight apparatus of pterygote insects exemplifies an energetically and metabolically demanding anatomical system (Mole & Zera 1993, 1994). The energy obtained from nutritional resources is consumed to a high degree by the maintenance of functional flight muscles in fully winged crickets, whereas in short-winged morphs of the same species this energy is more heavily invested in building up biomass in the ovaries (Mole & Zera 1993). However, this example of a selective trade-off between flight-capability and fecundity is by far not the only reason why wings were lost so many times independently within Pterygota. Wing loss is often correlated with ecological circumstances: e.g. environmental stability in isolated habitats. For instance, in cave communities dispersal does not represent an essential part of population survival. In deserts and other extreme habitats the energetic cost of flight is too high to maintain wings (reviewed in Wagner & Liebherr 1992).
In my thesis, I studied the morphological consequences associated with wing loss (Chapter 1, 2 and 3). Anatomical adaptations towards flightlessness exhibit a high degree of homogeneity within major polyneopteran lineages like Caelifera (Snodgrass 1929; Albrecht 1953; de Zolessi 1968), Xenonomia (Walker 1938; Wipfler *et al.* 2015), and Euphasmatodea (Klug 2008). As outlined in detail in chapter 1, major polyneopteran lineages differ in the set of tergopleural muscles. Nevertheless, a reduction in the number of direct flight muscles can usually be observed between winged and wingless representatives of the same taxon, e.g. in Phasmatodea (Klug 2008) and Zoraptera (Friedrich & Beutel 2008). However, no correlation can be found between flight capability and the number of direct flight muscles in winged polyneopteran representatives. This supports the assumption that flight capability and performance of insects do not only depend on the actual set and/or quantity of direct and indirect flight muscles, but also on the biomass of flight muscles (Marden 2000).

I compared the similarities and differences in the thoracic morphology of several wingless ensiferans. These include representative taxa of major ensiferan lineages, such as the cave cricket *Troglophilus* (Chapter 1), the dune cricket *Comicus* (Chapter 2), the Jerusalem cricket *Stenopelmatus*, and the king crickets *Papuaistus* and *Hemideina* (the latter three in Chapter 3). Some shared morphological modifications in the thoracic morphology of wingless Ensifera can now be proposed: wing base sclerites are absent, phragmata are less extensive, the set of direct flight muscles (tergopleural muscles) is reduced, and some indirect flight muscles (IIspm1 and IIdvm1) are absent. However, specific modifications like the set of retained tergopleural muscles differ slightly in these taxa. In *Stenopelmatus* (Stenopelmatidae) and *Papuaistus* (Anostostomatidae) the tergopleural muscles tpm9 and tpm10 are retained in the pterothorax. In contrast, in *Troglophilus* (Rhaphidophoridae) and *Hemideina* (Anostostomatidae) only tpm10 is present, while in *Comicus* (Schizodactylidae) not a single tergopleural muscle is developed. Although wing loss largely follows a similar morphological pattern within the Ensifera, the slight differences observed within a respective taxon (e.g. Anostostomatidae) support the hypothesis of multiple independent losses of wings in Ensifera. An interesting case in this regard represents the peculiar morphology of the winglessdune cricket *Comicus*, in which the complete loss of tergopleural muscles is shown to be a consequence of unique morphological adaptations related to its harsh and ecologically extreme habitat (Chapter 2).

Wagner and Liebherr (1992) pointed out that several morphological modifications are closely associated with flight loss, of which one deserves special attention with regard to the Orthoptera: the enhancement of jumping ability. This correlation is explained based on descriptions of some brachypterous moths that live on subantarctic islands (Wagner & Liebherr 1992). They possess enlarged hind femora enabling a 'grasshopper-like' jumping (Wagner & Liebherr 1992). However, Wagner and Liebherr (1992) do not mention which of these modifications, flight loss or enhanced jumping capability, preceded and, in consequence, triggered the other. In Orthoptera, evidence from the fossil record suggests that stemgroup orthopterans already possessed jumping hindlegs, but also had pronounced wings (Béthoux & Nel 2001, 2002). Consequently, the jumping hindleg must have evolved first in Orthoptera, and wings were subsequently lost. Indeed, since many orthopteran species primarily move by jumping, their flight ability and performance

become of secondary importance (Beier 1972). The presence of jumping hindlegs in stemgroup Orthoptera thus enabled an alternate, less costly form of locomotion and led to numerous convergent losses of wings and flight capability. This might explain the relatively high proportion of brachypterous and wingless species among Orthoptera (Roff 1994).

The systematic placement of Orthoptera among Polyneoptera, and the internal relationships of Ensifera

Numerous studies on the phylogenetic relationships within the Polyneoptera lead to contradicting hypotheses about the sister group of Orthoptera. The cladistic analysis of 141 thoracic characters (sclerites, musculature, and wing base) for 39 terminal taxa resulted in a single minimum-length tree (Chapter 3). In contrast to phylogenetic hypotheses proposing paraphyletic Polyneoptera (Kjer 2004; Terry & Whiting 2005; Wipfler *et al.* 2011), the monophyly of Polyneoptera is supported corroborating the current research studies (Letsch & Simon 2013; Misof *et al.* 2014; Wipfler *et al.* 2015; Song *et al.* 2016). In the presented phylogenetic hypothesis, Orthoptera pertain to a clade also comprising Phasmatodea (stick and leaf insects), Dictyoptera (praying mantises, cockroaches and termites), and Xenonomia (heel walkers and ice crawlers). Although this clade is only weakly supported mainly by ambiguous (homoplasious) characters, the invagination point of the pleural arm in the pterothoracic segments, which lies more ventrad in direct proximity to the pleural condylus (ventrad on epimeron in Xenonomia) is a unique character of those taxa. This clade comprising the aforementioned taxa plus Embioptera finds also strong support in the most comprehensive insect phylogenomic study to date (Misof *et al.* 2014). However, in Embioptera and in the phasmid *Timema*, no distinct pleural arm is developed (Bharadwaj & Chadwick 1974; Klug 2008). Nevertheless, the muscle usually connecting the furcal arm with the respective pleural arm, M. furca-pleuralis (II/IIIspm2) is still present, inserting near the pleural condylus in both taxa (Klug 2008). Hence, the monophyly of a clade including Orthoptera, Dictyoptera, Phasmatodea, Embioptera and Xenonomia appears to be supported by this character that experienced modifications in *Timema* and Embioptera.

An analysis excluding characters of the wing and wing base led to fully unresolved relationships among the polyneopteran lineages, but does not have a large effect on the recovered relationships within the Orthoptera. This observation demonstrates that the wing base characters contain important information for uncovering the deep polyneopteran phylogeny (Yoshizawa 2011). On the other hand the selected remaining thoracic characters appear to be phylogenetically informative to unravel the relationships within the Orthoptera. In accordance with other phylogenetic studies (Misof *et al.* 2014; Song *et al.* 2015), Caelifera as well as Ensifera are found to form monophyletic entities. Within Ensifera, a basal split in the 'grylloid clade' (crickets and mole crickets) and 'tettigonioid clade' (katydids and the remaining subgroups) is supported. This is in congruence with previous phylogenetic hypotheses (Desutter-Grandcolas 2003; Song *et al.* 2015; Zhou *et al.* 2017). However, the herein presented relationships within the 'tettigonioid clade' are proposed for the first time. Bush-crickets and katydids (Tettigoniidae) are found to form the sister taxon to a clade comprising all the remaining tettigonioid taxa: Gryllacrididae, Schizodactylidae, Prophalangopsidae, Rhaphidophoridae, Stenopelmatidae, and Anostostomatidae. A monophyletic taxon 'Stenopelmatoidea' containing Stenopelmatidae, Gryllacrididae and Anostostomatidae (*sensu* Song *et al.* 2015) finds no support in the presented analysis. Instead, the presence of a triramous metafurca bearing an additional dorsal process next to the anterior and lateral one represents an unambiguous apomorphic character of a clade Stenopelmatidae + Rhaphidophoridae + Prophalangopsidae + Anostostomatidae. The most unexpected finding is the systematic placement of Prophalangopsidae. Due to a similar intraspecific communication mode by tegminal stridulation, Prophalangopsidae were previously assumed to be the sister group to Tettigoniidae (Gwynne 1995; Desutter-Grandcolas 2003). Although this sister group hypothesis was also rejected in a recent phylogeny based on molecular data (Song *et al.* 2015), the authors refrain from discussing the resulting alternative evolutionary scenarios of bioacoustics among Ensifera.

Implications for the evolution of bioacoustics within Ensifera

The novel hypothesis of ensiferan relationships forms the basis for a reinterpretation of evolutionary scenarios related to their communicating mechanisms and hearing

systems (Chapter 3). Desutter-Grandcolas (2003) offers a detailed study to evaluate general communicational strategies and systems within the Ensifera. Based on an intense literature survey, Desutter-Grandcolas (2003) proposes three different organization types describing the distribution of airborne communication mechanisms and the occurrence of tibial tympana among Ensifera. In contrast, based on the re-evaluation of literature data (Chapter 3) four alternate configurations were identified: (1) tegminal stridulatory apparatus and tympana both present (Gryllidae, Gryllotalpidae, Tettigoniidae, Prophalangopsidae); (2) femoro-abdominal stridulatory apparatus and tympana both present (Anostostomatidae in part: e.g. *Hemideina* and *Deinacrida*); (3) femoro-abdomi-nal stridulatory apparatus present and tibial tympana lacking (Schizodactylidae, Stenopelmatidae, Gryllacrididae, Anostostomatidae in part: e.g. *Hemiandrus*); (4) femoro-abdominal stridulatory apparatus and tibial tympana both lacking (Rhaphidophoridae).

Referring to Desutter-Grandcolas (2003), a combination of two factors that are directly related to the communicational context could explain such a pattern: first, a signal emitted by stridulation is either acoustic or vibratory (Virant-Doberlet & Cockl 2004). Second, signals in general may be intended for intraspecific or interspecific communication (Ewing 1989). These two factors then determine who are the receiver and the emitter, what information is transmitted, and whether auditory structures are necessary (Desutter-Grandcolas 2003). Interestingly, tegminal stridulation is mainly used in an intraspecific context (Otte 1992; Greenfield 1997; Desutter-Grandcolas 1997; Howard & Hill 2006), whereas femoro-abdominal stridulation is used in an interspecific context by the vast majority of ensiferans in which it is present (Field 2001). The novel hypothesis of ensiferan relationships proposes certain branching patterns that are in congruence with the latest analysis of molecular data (Song *et al.* 2015), thereby contradicting previous hypotheses based on morphological evidence (Gwynne 1995; Desutter-Grandcolas 2003). The key findings and the resulting interpretation for the evolution of bioacoustics are briefly out-lined in the following: (1) Prophalangopsidae is not forming the sister group to Tettigoniidae. The presence of a tegminal stridulatory apparatus as an intraspecific communicational form must have evolved independently in Prophalangopsidae. (2) Rhaphidophoridae is not forming the sister group to the remaining tettigonioid lineages, instead a close relationship to Prophalangopsidae, Anostostomatidae and Stenopelmatidae is assumed. The hypothesis of a basal position of Rhaphidophoridae within

Ensifera previously supported the scenario of a non-stridulating and non-hearing ensiferan ancestor, and a step-wise evolution of the hearing organs and related stridulatory mechanisms (Stritih & Stumpner 2009). The novel hypothesis instead demands the assumption of the absence of a stridulatory organ as well as the structure of their hearing organs bearing no *crista acustica* in the ancestral rhaphidophorid (Jeram *et al.* 1995; Strauß *et al.* 2014b) to be the consequence of secondary simplification. (3) Tettigoniidae, Prophalangopsidae and Anostostomatidae do not form a monophyletic taxon (*contra* Desutter-Grandcolas 2003). The occurrence of intraspecific femoro-abdominal stridulation in Anostostomatidae cannot exclusively be interpreted as an acoustic, primarily intraspecific mode of communication, as stated by Desutter-Grandcolas (2003). In addition, femoro-abdominal stridulation used in an intraspecific context is only known from a few tympanate anostostomatid representatives (*Hemideina* and *Deinacrida*: Field 1993, 2001; *Libanasidus*: Bateman & Toms 1998). Yet, conspecifics of the atympanate anostostomatid genus *Hemiandrus* communicate by substrate vibrations resembling the intraspecific communicational mode of the likewise atympanate Stenopelmatidae, Gryllacrididae and Rhaphidophoridae (Field & Glasgow 2001). This observations rather support the view that the usage of femoro-abdominal stridulation as an intraspecific communicational mode represents a secondary modifi-cation that evolved within the Anostostomatidae.

By taking additional information into account, like the morphology of stridulatory structures (Ragge 1955; Sharov 1968; Chamorro-Rengifo *et al.* 2014), physiology and anatomy of hearing organs (Strauß *et al.* 2014b) and associated structures like the morphology of the auditory spiracles and tracheae (Ander 1939; Schmidt & Römer 2013; Strauß *et al.* 2014a) a well-founded and comprehensible evolutionary scenario for the evolution of bioacoustics in Ensifera can be proposed. The presence of an acoustic intraspecific communicational mode, either femoro-abdominal or tegminal, is always accompanied by the presence of tympana in the foreleg. Differences in the structural components and performance of tegminal stridulation support the view of an independent origin of this intraspecific communicational mode in Gryllidae, Gryllotalpidae, Tettigoniidae and Prophalangopsidae (Ander 1939; Desutter-Grandcolas 1997, 2003). Apart from Rhaphidophoridae (Jeram *et al.* 1995), the hearing organ of all tettigonioid lineages consists of a subgenual, and an intermediate organ in addition

to a *crista acustica/ crista austica* homologue (Strauß *et al.* 2014b). The *crista acustica* homologue exclusively described in atympanate Ensifera, such as Schizodactylidae (Strauß & Lakes-Harlan 2010) or Gryllacrididae (Strauß & Lakes-Harlan 2008a) likely improves the sensitivity or detection of different vibration waves (Strauß & Lakes-Harlan 2008b). In summary, the last common ancestor of the 'tettigonioid clade' likely lacked an acoustic intraspecific mode of communication and did not exhibit tympana in the forelegs, but likely had a tripartite tibial organ with a *crista acustica* homologue enhancing the plesiomorphic intraspecific communicational mode by substrate vibration. Consequently, this increased sensitivity towards vibrational signals of the tibial organ might have served as a precursor (by some authors improperly referred to as 'preadaptation') for the independent evolution of tympana and further assisting auditory structures such as hearing tracheae in those taxa that developed an intraspecific acoustic communicational mechanism.

Conclusions and future work

The presented thesis is an essential contribution towards a deeper understanding of the evolution of thoracic characters within Polyneoptera, and Orthoptera in particular. Yet, due the limited taxon sampling, it must still be considered as a first step providing the basis for more extensive future studies. The phylogenetic reconstruction of an evolutionary lineage based on characters of a single anatomical system can be impeded by functional constraints, parallel losses caused by a potential trend of simplification and also by diverse specializations occurring in the outgroup taxa chosen (Friedrich & Beutel 2010). In subsequent studies, morphological characters of the thoracic skeleton of representatives of Polyneoptera should be combined with available data on the morphology of other body parts, such as the head (Wipfler *et al.* 2011; Friedemann *et al.* 2012) and tarsal attachment structures (Beutel & Gorb 2006, 2008). In addition, much more research is needed on character systems currently not sufficiently studied in a comprehensive approach, like the preabdomen (Klug & Bradler 2006; Klug & Klass 2007) or genitalia (Klass & Ulbricht 2009; Chamorro-Rengifo & Lopes-Andrade 2014; Gorochov 2014). Nonetheless, simply adding more morphological data to a dataset can only partly compensate for misinterpretations of character transformations caused by a high degree of homoplasy, character loss and/or reversals (Wiens 2004). Simulation

studies have confirmed the benefits of an increased taxon sampling for phylogenetic accuracy in morphological studies, especially outlining the importance of sampling multiple species when inferring relationships among higher taxa (Wiens 1998). With regard to the presented survey, more research on the morphology of yet neglected ensiferan taxa like Stenopelmatidae or Gryllacrididae, for which only a single representative is included in the current thesis, is needed to arrive at a comprehensive understanding of character variability within the respective lineage.

The thoracic characters of Orthoptera that are shown to have a phylogenetic signal are in many cases related to the organization and anatomy of the chitinous exoskeleton, like the triramous structure of the metafurca in Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae, and Anostostomatidae. When examined, these skeletal characters are easy to be recognized and could effortlessly be coded for numerous ensiferan representatives. Micro-computed tomography is an innovative non-invasive morphological technique providing a convenient possibility for the investigation of insects (Friedrich *et al.* 2013). Without causing any mechanical damage, this technique even allows to investigate dried or alcohol-preserved material, allowing access to the examination of specimens, even valuable type material, stored in worldwide museum collections.

Revealing phylogenetic relationships based on morphological characters is limited, and is nowadays largely replaced by molecular phylogenies. Nevertheless, morphology still plays an essential role in visualizing evolutionary history on the phenotypic level by adding further explanations on form and function of certain morphological structures, as well as their evolutionary changes and modifications (Friedrich *et al.* 2013; Giribet 2015). In this thesis, this complex interaction of phylogeny, morphology and behavior is elucidated by the interpretation of evolutionary scenarios related to the origin of bioacoustics within the Ensifera. To find further arguments supporting the herein proposed evolutionary scenario of an independent origin of intraspecific communication in Ensifera further studies on their mating and defensive behavior is important. In Schizodactylidae for example a femoro-abdominal (Khattar 1972; Irish 1986) as well as an alternative femoro-elytral stridulatory apparatus (Mason 1961) are described, but information on the behavioral context, in which both stridulatory mechanism are alternatively used, is

lacking (Strauß & Lakes-Harlan 2010). The hypothesis of a secondary simplification of the hearing organ in Rhaphidophoridae is mainly built upon the investigation of a single species: *Troglophilus neglectus* (Jeram *et al.* 1995; Strauß *et al.* 2014b). It was previously demonstrated that animals living in isolated habitats such as caves exhibit a high degree of reduction and simplification in their body plans (Wagner & Liebherr 1992; Marques & Gnaspini 2001). All Rhaphidophoridae are reported to prefer humid habitats and have a nocturnal lifestyle (Rentz 1996). Nonetheless, as *Troglophilus* is a strict cave dweller (Karaman *et al.* 2011), the examination of more widespread, mainly free-living rhaphidophorids from the rain forests of Australia and New Zealand (Rentz 1996) may lead to useful hints regarding the groundplan morphology of their tibial organs.

References

Albrecht, F. O. 1953. *The Anatomy of the Migratory Locust*. University of London, Athlone Press, Western Printing Services Ltd., London, 1-118 pp.

Ander, K. 1939. Vergleichend-anatomische und phylogenetische Studien über die Ensifera (Saltatoria). *Opuscula Entomologica Supplementum II*, 1–306.

Bateman, P. & Toms, R. 1998. Mating, mate guarding and male-male relative strength assessment in an African king cricket (Orthoptera: Mimnermidae). *Transactions of the American Entomological Society*, **124**, 69–75.

Beier, M. 1972. Saltatoria (Grillen und Heuschrecken). *In*: Helmcke, J. G., Starck, D. & Wermuth, H. (eds) *Handbuch Der Zoologie*. Walter De Gruyter & Co, Berlin, 1–217.

Béthoux, O. & Nel, A. 2001. Venation pattern of Orthoptera. *Journal of Orthoptera Research*, **10**, 195–198.

Béthoux, O. & Nel, A. 2002. Venation pattern and revision of Orthoptera *sensu nov*. and sister groups. Phylogeny of palaeozoic and mesozoic Orthoptera *sensu nov*. *Zootaxa*, **96**, 1–88.

Beutel, R. G. & Gorb, S. N. 2006. A revised interpretation of the evolution of attachment structures in Hexapoda with special emphasis on Mantophasmatodea. *Arthropod Systematics & Phylogeny*, **64**, 3–25.

Beutel, R. G. & Gorb, S. N. 2008. Evolutionary scenarios for unusual attachment devices of Phasmatodea and Mantophasmatodea (Insecta). *Systematic Entomology*, **33**, 501–510.

Bharadwaj, R. K. & Chadwick, L. E. 1974. Postembryonic development of the cervico-thoracic skeleton of *Euborellia annulipes* (Lucas) (Dermaptera: Labiduridae). *Journal of Morphology*, **143**, 457–473.

Carpentier, F. 1921. Sur l'endosquelette prothoracique de *Gryllotalpa vulgaris*. *Bulletin de la Classe des Sciences, Académie Royale de Belgique*, **7**, 125–134.

Carpentier, F. 1936. Le thorax et ses appendices chez les vrais et les faux Gryllotalpides. *Mémoires du Musée Royale d'Histoire Naturelle de Belgique. 2ème Série*, **4**, 3–86.

Chamorro-Rengifo, J. & Lopes-Andrade, C. 2014. The phallus in Tettigoniidae (Insecta: Orthoptera: Ensifera): revision of morphology and terminology, and discussion on its taxonomic importance and evolution. *Zootaxa*, **3815**, 151–199.

Chamorro-Rengifo, J., Braun, H. & Lopes-Andrade, C. 2014. The secret stridulatory file under the right tegmen in katydids (Orthoptera, Ensifera, Tettigonioidea). *Zootaxa*, **3821**, 590–596.

de Zolessi, L. C. 1968. Morphologie, endosquelette et musculature d'un acridien aptère (Orthoptera: Proscopiidae). *Transactions of the Royal Entomological Society of London*, **120**, 55–113.

Desutter-Grandcolas, L. 1997. A phylogenetic analysis of the evolution of the stridulatory apparatus in true crickets (Orthoptera, Grylloidea). *Cladistics*, **13**, 101–108.

Desutter-Grandcolas, L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta*, **32**, 525–561.

Ewing, A. 1989. *Arthropod Bioacoustics: Neurobiology and Behaviour*. Edinburgh University Press, Edinburgh, 260pp.

Field, L. H. 1993. Observations on stridulatory, agonistic, and mating behaviour of (Stenopelmatidae : Orthoptera), the rare Banks Peninsula weta. *New Zealand Entomologist*, **16**, 68–74.

Field, L. H. 2001. Stridulatory mechanisms and associated behaviour in New Zealand Wetas. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 271–295.

Field, L. H. & Glasgow, S. 2001. Defence behaviour. *In*: Field, L. H. (ed.) *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, New York, 297–316.

Friedemann, K., Wipfler, B., Bradler, S. & Beutel, R. G. 2012. On the head morphology of *Phyllium* and the phylogenetic relationships of Phasmatodea (Insecta). *Acta Zoologica*, **93**, 184–199.

Friedrich, F. & Beutel, R. G. 2008. The thorax of *Zorotypus* (Hexapoda, Zoraptera) and a new nomenclature for the musculature of Neoptera. *Arthropod Structure & Development*, **37**, 29–54.

Friedrich, F. & Beutel, R. G. 2010. Goodbye Halteria? The thoracic morphology of Endopterygota (Insecta) and its phylogenetic implications. *Cladistics*, **26**, 579–612.

Friedrich, F., Matsumura, Y., Pohl, H., Bai, M., Hörnschemeyer, T. & Beutel, R. G. 2013. Insect morphology in the age of phylogenomics: innovative techniques and its future role in systematics. *Entomological Science*, **17**, 1–24.

Giribet, G. 2015. Morphology should not be forgotten in the era of genomics—a phylogenetic perspective. *Zoologischer Anzeiger - A Journal of Comparative Zoology*, **256**, 96–103.

Gorochov, A. V. 2014. Evolution and taxonomic significance of the copulatory apparatus in Ensifera (Orthoptera). Part 1: General concepts and origin. *Zoosystematica Rossica*, **23**, 197–209.

Greenfield, M. D. 1997. Acoustic communication in Orthoptera. *In*: Gangwere, S. K., Muralirangan, M. C. & Muralirangan, M. (eds) *The Bionomics of Grasshoppers, Katydids and Their Kin*. CAB International, Wallingford, New York, 197–230.

Gurney, A. B. 1935. *The External Morphology and Phylogenetic Position of the Woodland Cave Cricket (*Ceuthophilus Brevipes *Scudder; Orthoptera; Tettigoniidæ)*. University of Massachusetts Amherst, 1-46 pp.

Gwynne, D. T. 1995. Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research*, **4**, 203–218.

Howard, D. R. & Hill, P. S. M. 2006. Morphology and calling song characteristics in *Gryllotalpa major* Saussure (Orthoptera: Gryllotalpidae). *Journal of Orthoptera Research*, **15**, 53–57.

Irish, J. 1986. The species of *Comicus* Brunner v. Wattenwyl (Orthoptera: Schizodactylidae) with a discussion of their origin. *Navorsinge van die Nasionale Museum Bloemfontein*, **5**, 253–276.

Jeram, S., Rössler, W., Cokl, A. & Kalmring, K. 1995. Structure of atympanate tibial organs in legs of the cave-living Ensifera, *Troglophilus neglectus* (Gryllacridoidea, Raphidophoridae). *Journal of Morphology*, **223**, 109–118.

Karaman, I., Hammouti, N., Pavićević, D., Kiefer, A., Horvatović, M. & Seitz, A. 2011. The genus *Troglophilus* Krauss, 1879 (Orthoptera: Rhaphidophoridae) in the west Balkans. *Zoological Journal of the Linnean Society*, **163**, 1035–1063.

Khattar, N. 1972. A description of the adult and the nymphal stages of *Schizodactylus monstrosus* (Drury) (Orthoptera). *Journal of Natural History*, **6**, 589–600.

Khattar, N. & Srivastava, R. P. 1962. Morphology of the pterothorax of *Schizodactylus monstrosus* Don. (Orthoptera). *Journal of the Zoological Society of India*, **14**, 93–108.

Kjer, K. 2004. Aligned 18S and insect phylogeny. *Systematic Biology*, **53**, 506–514.

Klass, K. D. & Ulbricht, J. 2009. The female genitalic region and gonoducts of Embioptera (Insecta), with general discussions on female genitalia in insects. *Organisms Diversity and Evolution*, **9**, 115–154.

Klug, R. 2008. *Anatomie des Pterothorax der Phasmatodea, Mantophasmatodea und Embioptera und seine Bedeutung für die Phylogenie der Polyneoptera (Insecta).* Georg-August-Universität Göttingen, 1-126 pp.

Klug, R. & Bradler, S. 2006. The pregenital abdominal musculature in phasmids and its implications for the basal phylogeny of Phasmatodea (Insecta: Polyneoptera). *Organisms Diversity and Evolution*, **6**, 171–184.

Klug, R. & Klass, K. D. 2007. The potential value of the mid-abdominal musculature and nervous system in the reconstruction of interordinal relationships in lower Neoptera. *Arthropod Systematics and Phylogeny*, **65**, 73–100.

Letsch, H. & Simon, S. 2013. Insect phylogenomics: new insights on the relationships of lower neopteran orders (Polyneoptera). *Systematic Entomology*, **38**, 783–793.

Marden, J. H. 2000. Variability in the size, composition, and function of insect flight muscles. *Annual Reviews of Physiology*, **62**, 157–178.

Marques, A. C. & Gnaspini, P. 2001. The problem of characters susceptible to parallel evolution in phylogenetic reconstructions: suggestion of a practical method and its application to cave animals. *Cladistics*, **17**, 371–381.

Maskell, F. G. 1927. The anatomy of *Hemideina thoracica*. *Transactions of the Royal Society of New Zealand*, **57**, 637–669.

Mason, J. B. 1961. Stridulatory mechanism in the family Schizodactylidae (Orth. Gryllacridoidea). *Eos*, **37**, 505–508.

Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, a., Mayer, C., Frandsen, P. B., Ware, J., Flouri, T., Beutel, R. G., Niehuis, O., Petersen, M., Izquierdo-Carrasco, F., Wappler, T., Rust, J., Aberer, a. J., Aspock, U., Aspock, H., Bartel, D., Blanke, a., Berger, S., Bohm, a., Buckley, T. R., Calcott, B., Chen, J., Friedrich, F., Fukui, M., Fujita, M., Greve, C., Grobe, P., Gu, S., Huang, Y., Jermiin, L. S., Kawahara, a. Y., Krogmann, L., Kubiak, M., Lanfear, R., Letsch, H., Li, Y., Li, Z., Li, J., Lu, H., Machida, R., Mashimo, Y., Kapli, P., McKenna, D. D., Meng, G., Nakagaki, Y., Navarrete-Heredia, J. L., Ott, M., Ou, Y., Pass, G., Podsiadlowski, L., Pohl, H., von Reumont, B. M., Schutte, K., Sekiya, K., Shimizu, S., Slipinski, a., Stamatakis, a., Song, W., Su, X., Szucsich, N. U., Tan, M., Tan, X., Tang, M., Tang, J., Timelthaler, G., Tomizuka, S., Trautwein, M., Tong, X., Uchifune, T., Walzl, M. G., Wiegmann, B. M., Wilbrandt, J., Wipfler, B., Wong, T. K. F., Wu, Q., Wu, G., Xie, Y., Yang, S., Yang, Q., Yeates, D. K., Yoshizawa, K., Zhang, Q., Zhang, R., Zhang, W., Zhang, Y., Zhao, J., Zhou, C., Zhou, L., Ziesmann, T., Zou, S., Xu, X., Yang, H., Wang, J., Kjer, K. M. & Zhou, X. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.

Mole, S. & Zera, A. J. 1993. Differential allocation of resources underlies the dispersal-reproduction trade-off in the wing-dimorphic cricket, *Gryllus rubens*. *Oecologia*, **93**, 121–127.

Mole, S. & Zera, A. J. 1994. Differential resource consumption obviates a potential flight-fecundity trade-off in the sand cricket (*Gryllus firmus*). *Functional Ecology*, **8**, 573–580.

Otte, D. 1992. Evolution of cricket songs. *Journal of Orthoptera Research*, **1**, 25–49.

Ragge, D. R. 1955. *The Wing-Venation of the Orthoptera Saltatoria. With Notes on Dictyopteran Wing-Venation.* British Museum (Natural History), London, 1-159 pp.

Rentz, D. C. F. 1996. *Grasshopper Country : The Abundant Orthopteroid Insects of Australia*. University of New South Wales Press, Sydney, Australia, 284 pp.

Richards, A. M. 1955. The anatomy and morphology of the cave-orthopteran *Macropathus filifer* Walker, 1869. *Transactions of the Royal Society of New Zealand*, **83**, 405–452.

Roff, D. A. 1994. The evolution of flightlessness: is history important? *Evolutionary Ecology*, **8**, 639–657.

Schmidt, A. K. & Römer, H. 2013. Diversity of acoustic tracheal system and its role for directional hearing in crickets. *Frontiers in Zoology*, **10**, 61.

Sharov, A. G. 1968. Phylogeny of the Orthopteroidea. *Transactions of the Institute of Paleontology. Academy of Sciences of the USSR*, **118**, 1–251.

Snodgrass, R. E. 1929. The thoracic mechanism of a grasshopper, and its antecedents. *Smithsonian Miscellaneous Collections*, **82**, 1–111.

Song, H., Am, C., Marta, M., Desutter-, L., Heads, S. W., Huang, Y., Otte, D. & Whiting, M. F. 2015. 300 million years of diversification : elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics*, **31**, 621–651.

Song, N., Li, H., Song, F. & Cai, W. 2016. Molecular phylogeny of Polyneoptera (Insecta) inferred from expanded mitogenomic data. *Scientific Reports*, **6**, 36175.

Strauß, J. & Lakes-Harlan, R. 2008a. Neuroanatomy and physiology of the complex tibial organ of an atympanate ensiferan, *Ametrus tibialis* (Brunner von Wattenwyl, 1888) (Gryllacrididae, Orthoptera) and evolutionary implications. *Brain, Behavior and Evolution*, **71**, 167–180.

Strauß, J. & Lakes-Harlan, R. 2008b. Neuroanatomy of the complex tibial organ of *Stenopelmatus* (Orthoptera: Ensifera: Stenopelmatidae). *The Journal of Comparative Neurology*, **511**, 81–91.

Strauß, J. & Lakes-Harlan, R. 2010. Neuroanatomy of the complex tibial organ in the splay-footed cricket *Comicus calcaris* Irish 1986 (Orthoptera: Ensifera: Schizodactylidae). *The Journal of Comparative Neurology*, **518**, 4567–4580.

Strauß, J., Lehmann, A. W. & Lehmann, G. U. C. 2014a. Sensory evolution of hearing in tettigoniids with differing communication systems. *Journal of Evolutionary Biology*, **27**, 200–213.

Strauß, J., Stritih, N. & Lakes-Harlan, R. 2014b. The subgenual organ complex in the cave cricket *Troglophilus neglectus* (Orthoptera: Rhaphidophoridae): comparative innervation and sensory evolution. *Royal Society Open Science*, **1**, 140240.

Stritih, N. & Stumpner, A. 2009. Vibratory interneurons in the non-hearing cave cricket indicate evolutionary origin of sound processing elements in Ensifera. *Zoology*, **112**, 48–68.

Terry, M. D. & Whiting, M. F. 2005. Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics*, **21**, 240–257.

Virant-Doberlet, M. & Cockl, A. 2004. Vibrational communication in insects. *Neotropical Entomology*, **33**, 121–134.

Voss, F. 1905a. Über den Thorax von *Gryllus domesticus*. Erster Teil. Das Skelett. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (2)**, 268–514.

Voss, F. 1905b. Über den Thorax von *Gryllus domesticus*. Zweiter Teil. Die Muskulatur. *Zeitschrift für Wissenschaftliche Zoologie*, **78 (3)**, 355–521.

Wagner, D. L. & Liebherr, J. K. 1992. Flightlessness in Insects. *Trends in Ecology & Evolution*, **7**, 216–220.

Walker, E. M. 1938. On the anatomy of *Gylloblatta campodeiformis* Walker. 3. Exoskeleton and musculature of the neck and thorax. *Annals of the Entomological Society of America*, **31**, 588–640.

Wiens, J. J. 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology*, **53**, 653–661.

Wiens, J. J. 1998. The accuracy of methods for coding and sampling higher-level taxa for phylogenetic analysis: a simulation study. *Systematic Biology*, **47**, 397–413.

Wipfler, B., Machida, R., Müller, B. & Beutel, R. G. 2011. On the head morphology of Grylloblattodea (Insecta) and the systematic position of the order, with a new nomenclature for the head muscles of Dicondylia. *Systematic Entomology*, **36**, 241–266.

Wipfler, B., Klug, R., Ge, S.-Q., Bai, M., Göbbels, J., Yang, X.-K. & Hörnschemeyer, T. 2015. The thorax of Mantophasmatodea, the morphology of flightlessness, and the evolution of the neopteran insects. *Cladistics*, **31**, 50–70.

Yoshizawa, K. 2011. Monophyletic Polyneoptera recovered by wing base structure. *Systematic Entomology*, **36**, 377–394.

Zhou, Z., Zhao, L., Liu, N., Guo, H., Guan, B., Di, J. & Shi, F. 2017. Towards a higher-level Ensifera phylogeny inferred from mitogenome sequences. *Molecular Phylogenetics and Evolution*, **108**, 22–33.

Zusammenfassung

Die Hauptziele der vorliegenden Arbeit liegen in (1) einer detaillierten morphologischen Studie von Skelett und Muskulatur des Thorax von Orthopteren, (2) einer vergleichenden Studie von verschiedenen Polyneoptera und insbesondere der Ensifera über die morphologischen Veränderungen im Zusammenhang mit sekundärer Flügellosigkeit, (3) der phylogenetischen Rekonstruktion der Verwandtschaftsverhältnisse innerhalb der Ensifera basierend auf Merkmalen des thorakalen Skeletts und seiner Muskulatur, (4) einer Neuinterpretation zur Evolution der Bioakustik innerhalb der Ensifera.

Die Morphologie des Skeletts und der Muskulatur des Thorax von 23 Arten der Orthoptera wurde im Detail untersucht, wobei repräsentative Vertreter aller wichtigen Taxa der Ensifera einbezogen worden sind. Diese umfangreiche vergleichende Studie diente dabei als Basis für eine sorgfältige Rekonstruktion des Grundmusters dieses Merkmalskomplexes für die Orthoptera. Sowohl die Morphologie des Skeletts als auch die der Muskulatur offenbart zum Teil große Unterschiede zwischen den beiden Großgruppen der Orthoptera, den Caelifera (Kurzfühlerschrecken) und den Ensifera (Langfühlerschrecken). Die sekundäre Flügellosigkeit ist ein weitverbreitetes Phänomen unter den geflügelten Insekten und beeinflusst vor allem die Anatomie des Thorax, insbesondere die des Skeletts und der Muskulatur. Durch den Vergleich der Morphologie des Thorax verschiedener flügelloser Vertreter der Polyneoptera kann gezeigt werden, dass anatomische Anpassungen an die Flügellosigkeit, insbesondere der Flugmuskulatur, innerhalb von Insektentaxa (wie zum Beispiel den Ensifera, Caelifera oder auch Euphasmatodea) sehr einheitlich sind. Allerdings können spezifische Anpassungen zwischen diesen einzelnen Linien stark variieren, was auf verschiedenartige Funktionen der verbliebenen Flugmuskeln nach dem Verlust der Flügel hindeutet.

Da die systematische Stellung der Orthoptera innerhalb der Polyneoptera derzeit nicht ausreichend geklärt ist, wurden neben Vertretern aller Gruppen der Polyneoptera auch repräsentative Arten der Holometabola, Paraneoptera und Palaeoptera in die kladistische Analyse einbezogen. Diese basierte auf der Auswertung von 141 Merkmalen des Thorax und führte zu einer einzigen sparsamsten Verwandtschaftshypothese. Innerhalb der als monophyletisch erkannten Polyneoptera stehen die Orthoptera in einem nahen Verwandtschaftsverhältnis zu den Xenonomia (Grylloblattodea + Mantophasmatodea),

Dictyoptera und Phasmatodea. Die Ensifera zeigen eine basale Aufspaltung in zwei Linien: Grillen und Maulwurfsgrillen (Grylloideen) und Laubheuschrecken sowie ihre Verwandten (Tettigonioideen). Die Tettigoniidae (Laubheuschrecken) bilden das Schwestertaxon zu einem Taxon, dass die Gryllacrididae, Schizodactylidae, Stenopelmatidae, Rhaphidophoridae, Prophalangopsidae und Anostostomatidae umfasst. Die monophyletische Abstammung der letztgenannten Gruppen stützt sich auf das Vorhandensein eines ausgeprägten nach posterior ragenden Profurkalarmes (konvergent bei den Grylloblattodea) und einem paarigen nach hinten gerichteten Fortsatzes der gestielten Prospina (Merkmalsumkehr bei den Prophalangopsidae). Weitere wichtige Ergebnisse zur internen Phylogenie der Ensifera nebst darauf aufbauenden Schlussfolgerungen für die Evolution der Bioakustik sind im Folgenden kurz aufgeführt: (1) Die Prophalangopsidae bilden nicht das Schwestertaxon zu den Tettigoniidae. Die tegminale Stridulation als eine Form der intraspezifischen Kommunikation muss demnach mindestens dreimal unabhängig voneinander entstanden sein: bei den Gryllidae + Gryllotalpidae, Tettigoniidae und Prophalangopsidae. (2) Die Rhaphidophoridae bilden nicht das Schwestertaxon zu den verbleibenden Gruppen der Tettigonioideen. Stattdessen wird eine nahe Verwandtschaft zu den Prophalangopsidae, Anostostomatidae und Stenopelmatidae favorisiert, da alle Vertreter das ihnen eigene Merkmal einer dreigabeligen Metafurca besitzen. Die ursprüngliche Hypothese einer basalen Stellung der Rhaphidophoridae innerhalb der Tettigonioideen unterstützte bislang die Theorie eines tauben und nicht-stridulierenden gemeinsamen Vorfahrens der Ensifera und eine schrittweise verlaufende Evolution ihrer Gehörorgane und der damit verbundenen Stridulationsmechanismen hin zu singenden und hörenden Vertretern wie beispielsweise den Tettigoniidae. Basierend auf der neuen Verwandtschaftshypothese muss aber davon ausgegangen werden, dass es sich bei der Morphologie der Gehörorgane von Rhaphidophoriden, die keine Spuren einer Crista acustica zeigen, um eine sekundäre Vereinfachung handelt. (3) Tettigoniidae, Prophalangopsidae und Anostostomatidae bilden keine monophyletische Gruppierung. Das Vorhandensein von akustischer intraspezifischer Kommunikation in diesen drei Taxa, sei es durch tegminale oder femoro-abdominale Stridulation, kann demnach nicht als plesiomorph für die einzelnen Gruppen interpretiert werden. Vielmehr handelt es sich dabei um unabhängig entstandene apomorphe Merkmale der Tettigoniidae, Prophalangopsidae und einer Teilgruppe der Anostostomatidae.

Zusammenfassend liefert diese Arbeit viele zusätzliche Erkenntnisse über die Morphologie eines vielschichtigen anatomischen Merkmalskomplexes. Die vorliegende Arbeit repräsentiert einen essentiellen Schritt zum tieferen Verständnis der Evolution von Thoraxmerkmalen und damit assoziierten funktionellen Anpassungen innerhalb der Polyneoptera und insbesondere der Orthoptera. Denn obwohl kladistische Analysen morphologischer Merkmale heutzutage durch solche molekularer Merkmale abgelöst werden, bleibt die Morphologie weiterhin ein Wissenschaftszweig, der als wichtigstes Instrument zur Veranschaulichung evolutionärer Prozesse dient, Form und Funktion morphologischer Transformationen erklärt und Evolution dadurch greifbar macht.

List Of Publications

Leubner, F., Bradler, S. & Wipfler, B. 2017. The thoracic morphology of the wingless dune cricket *Comicus calcaris* (Orthoptera: Schizodactylidae): Novel apomorphic characters for the group and adaptations to sand desert environments. *Arthropod Structure & Development*, 46, 449–461. DOI: 10.1016/j.asd.2017.03.006

Leubner, F., Hörnschemeyer, T. & Bradler, S. 2016. The thorax of the cave cricket *Troglophilus neglectus*: anatomical adaptations in an ancient wingless insect lineage (Orthoptera: Rhaphidophoridae). *BMC Evolutionary Biology*, 16, 39. DOI: 10.1186/s12862-016-0612-5

Goldberg, J., Bresseel, J., Constant, J., Kneubühler, B., **Leubner, F.**, Michalik, P & Bradler, S. 2015. Extreme convergence in egg-laying strategy across insect orders. *Scientific Reports*, 5, 7825. DOI: 10.1038/srep07825

Danksagung

Allen voran möchte ich mich bei meinem Betreuer PD Dr. Sven Bradler bedanken, der mir auf meinem Weg zur Wissenschaftlerin mit seinem Rat stets zur Seite gestanden hat: sei es bei den ersten holperigen Versuchen beim Verfassen von Manuskripten oder der manchmal nicht enden wollenden Korrespondenz mit Fachjournalen. Auch danke ich dir für die vielen Freiheiten und die Möglichkeit, mein wissenschaftliches Ich selbst zu definieren.

Prof. Dr. Rainer Willmann danke ich für die Übernahme der Aufgabe des Koreferenten und die großartige Möglichkeit als Mitarbeiterin in seiner Abteilung nicht nur die Wissenschaft, sondern auch die Lehre als Passion zu entdecken.

Ich danke PD Dr. Thomas Hörnschemeyer für die Unterstützung und Hilfestellung im Umgang mit den 3D-Rekonstruktionsprogrammen.

Ich danke Prof. Dr. Rolf Beutel und seiner Arbeitsgruppe für die herzliche Aufnahme während meines Aufenthalts in Jena sowie die lehrreichen Einblicke in die wissenschaftliche Arbeit mit Insekten, die den Startschuss meiner Doktorarbeit bedeuteten. Im Speziellen danke ich Dr. Benjamin Wipfler für die Bereitstellung von Material und das Anfertigen von CT-Datensätzen, die fruchtvolle Zusammenarbeit am zweiten Manuskript, sowie das stets offene Ohr und die aufbauenden Worte bei unseren zahlreichen Telefonaten.

Ich danke Dr. Christian Fischer für die kritische Auseinandersetzung mit meiner wissenschaftlichen Arbeit, den vielen Denkanstößen und philosophischen Exkursen während mehr oder weniger lang andauernden „Schaffens“pausen vor dem Haupteingang der Zoologie.

Ich danke meiner besten Freundin Anita, die trotz der uns trennenden Entfernung immer ganz nah bei mir war.

Großer Dank gebührt auch allen anderen Freunden, alte und neu gewonnene, die in dieser langen Zeit hinter mir standen. Denjenigen, die in der anfangs einsamen Zeit in Göttingen lange Wege auf sich nahmen, um bei mir zu sein. Denjenigen, die mir die Stadt mit all seinen Facetten näher brachten. Und denjenigen, die sich die Nächte mit mir um die Ohren geschlagen haben.

Vielen Dank an die Mitglieder von „Christian F. und die Kinder vom Busbahnhof Zoo“ für die schönen Stunden in unserem Proberaum, denn die Musik war und wird für mich immer einer großer Teil meines Lebens sein.

Mein größter Dank gilt meiner Familie, meinen Eltern Gabriela und André, meiner Schwester Sophie und meinen Großeltern Ute und Jochen. Seit dem Beginn meines Studiums habt ihr mich in allen Belangen unterstützt, stets hinter mir und meinen Entscheidungen gestanden und mir in Zeiten des Selbstzweifels die Kraft gegeben weiterzumachen.

Nicht zuletzt danke ich Andreas, meiner besseren Hälfte und Liebe meines Lebens. Du bist die Person, die am eigenen Leib spüren musste, wie sich eine Doktorarbeit mit all ihren Phasen auf das Leben außerhalb von Wissenschaft und Universität auswirkt. Ich danke dir für deine moralische Unterstützung, deinen ungebrochenen Glauben in meine Arbeit und deine Engelsgeduld.